

INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX



COMITÉ DE RÉDACTION

P. H. CHRISTENSEN, K. GÖSSWALD, P.-P. GRASSÉ,
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Volume I - Juillet 1954 - Numéro 3

MASSON & Cie, ÉDITEURS - PARIS

INSECTES SOCIAUX

Revue consacrée à l'étude de la Morphologie, de la Systématique et de la Biologie des Insectes sociaux.

Publiée sous les auspices de

L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX

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PRIX DE L'ABONNEMENT POUR 1954

France et Union Française : **3 000 frs.**

Étranger { Dollars U. S. A. : **9,25.**
 { Francs Belges : **460.**

Également payable au cours officiel
dans les autres monnaies.

Prix spécial pour les membres de l'Union internationale pour l'étude des Insectes sociaux.

France et Union Française : **2 000 frs.**

Étranger { Dollars : **5,75.**
 { Francs Belges : **286.**

Règlement : a) Chèque sur Paris d'une banque officielle.
 b) Virement par banque sur compte étranger.
 c) Mandat International.

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SOMMAIRE

Mémoires originaux.

Sulle proprietà antibatteriche del veleno di <i>Apis mellifica</i> L. (Hym. Apidæ), G. P. BRANGI, M. PAVAN.....	209
Quelques régulations sociales dans la construction chez les Abeilles, par ROGER DARCHEN	219
Untersuchungen zur Kastendetermination in der Gattung <i>Formica</i> . 3. Die Kas- tendetermination von <i>Formica rufa Rufo-pratensis minor</i> Gößw., von KARL GößWALD und KARLHEINZ BIER.....	229
A. Statistical Analysis of communication in <i>Apis mellifera</i> and a Comparison with Communication in other animals, by J. B. S. HALDANE and H. SPURWAY.	247
Untersuchungen über den Nährwert von Pollenersatzmitteln für die Honig- biene, von OSCAR WAHL.....	285
CORRESPONDANCE.....	293
NOUVELLES ESPÈCES DE TERMITES DÉCRITES AU COURS DES ANNÉES 1952 ET 1953.	295

Nouvelles de l'Union.

La vie des sections.....	297
Travaux publiés par des membres de l'Union.....	298

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TOME PREMIER

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120, boulevard Saint-Germain, PARIS-VI^e

1954

I

MÉMOIRES ORIGINAUX

SULLE PROPRIETÀ ANTIBATTERICHE DEL VELENO DI *APIS MELLIFICA* L. (HYM. APIDÆ)

G. P. BRANGI, M. PAVAN

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INTRODUZIONE

Nella biologia dell'Ape giocano un ruolo molto importante prodotti e secrezioni caratteristiche come il miele, il propoli, la cera, la pappa reale, il veleno. Non tutti questi prodotti e secrezioni sono stati compiutamente studiati dal punto di vista chimico e per le loro proprietà biologiche.

Fra le proprietà biologiche poco conosciute possiamo annoverare anche il potere antibatterico. Noi abbiamo raccolto la letteratura sul potere antibatterico del miele, del propoli, della pappa reale e del veleno e in una prossima nota esporremo i dati raccolti e ragionati anche in relazione alle ricerche sui fattori antibatterici di origine animale che uno di noi persegue da anni.

Non ci soffermiamo sugli studi compiuti da numerosi Autori sulla chimica del veleno e sulle sue varie proprietà biologiche poichè questi dati entreranno nella parte compilativa della prossima nota. In questa nota esponiamo invece i risultati delle nostre ricerche sul fattore antibatterico del veleno d'ape, che è tuttora assai scarsamente conosciuto.

Le notizie bibliografiche a questo proposito sono molto scarse. PHISALIX (1922) accenna genericamente all'inibizione di crescita di colture batteriche trattate con veleno di Ape.

SCHMIDT-LANGE (1941) impiegando per le ricerche un preparato farmaceutico (Forapin) contenente veleno d'Ape, riscontra attività antibatterica su streptococchi, stafilococchi, e in misura minore su *Bacterium coli*.

Nel 1948 PAVAN e NASCIMBENE, nel quadro delle ricerche sugli antibiotici di origine animale, riscontravano attività antibatterica con estratti di addomi di operaie. Tali estratti risultarono attivi su : *Vibrio comma*, *Ebertella typhosa*, *Mycobacterium phlei*. Estratti di teste e di toraci di

operaie risultarono inattivi. Nel 1949 PAVAN fa cenno dell'attività antibatterica di una frazione di veleno d'Ape.

Queste, a quanto ci risulta, sono le sole notizie che abbiamo sulle proprietà antibatteriche del veleno d'Ape.

Da quanto sopra è evidente che le cognizioni sull'attività antibatterica del veleno d'Ape sono del tutto preliminari. Scopo delle nostre ricerche fu di approfondire la conoscenza dell'attività antibatterica, determinare le prime caratteristiche fisiche del principio attivo, tentare una prima differenziazione rispetto al principio tossico detto apitossina.

Per questo abbiamo compiuto i seguenti gruppi di ricerche : 1) estrazione degli apparati velenosi con diversi solventi e saggio dell'attività su 10 specie batteriche ; 2) evidenziazione dell'attività antibatterica senza estrazione chimica, ma per diretta diffusione del principio attivo dall'apparato del veleno nel terreno colturale ; 3) determinazione della resistenza termica del principio attivo ottenuto con varie modalità estrattive ; 4) precipitazione alcoolica dell'estratto acquoso e tentativi di differenziazione rispetto al fattore tossico *apitossina*.

Tecniche di prelevamento del veleno e di saggio dell'attività antibatterica.

Per l'insieme degli esperimenti condotti abbiamo prelevato oltre 10.000 apparati del veleno. Per questo lavoro di raccolta abbiamo adottato metodi che sostanzialmente corrispondono a quelli più comunemente impiegati dagli Autori che hanno studiato l'argomento, o dai produttori di veleno a scopo terapeutico.

I metodi d'uso corrente sono i seguenti :

I: afferrata l'Ape tra due dita si esercita una debole pressione sull'addome ; in tal modo l'insetto spinge in fuori il pungiglione alla cui estremità compare una goccia di liquido che si raccoglie con un capillare. Si può raccogliere il veleno su un vetrino da orologio o su carta bibula ed essiccare nel vuoto conservando al riparo dalla luce. Se si vuol preparare una soluzione da iniettarsi all'istante, si immerge l'estremità del pungiglione con la sua goccia in acqua distillata. Operando in tal modo su un certo numero di insetti, si ottengono soluzioni a concentrazione varia, tenendo presente che ogni Ape fornisce mg. 0,2-0,4 di veleno.

II: dopo aver cloroformizzati gli insetti, si afferra con una pinza il pungiglione e si strappa. In tal modo vengono strappati oltre al pungiglione le ghiandole e il serbatoio del veleno e a volte anche una parte del tubo intestinale che però può essere agevolmente separato dal resto. L'apparato velenoso viene poi lavorato con vari metodi estrattivi a seconda dell'impiego che si vuol fare del veleno.

Nelle nostre ricerche abbiamo adottato soprattutto il metodo II.

Per quanto riguarda il saggio dell'attività antibatterica, la tecnica da noi impiegata è quella dell'agar-germi, con saggio degli estratti in pozzetto nel terreno colturale.

RICERCHE PERSONALI

I primi esperimenti furono diretti a ricercare l'attività antibatterica di estratti di apparati del veleno con vari solventi : acqua distillata, etere di petrolio, acetone, alcool etilico 96°. Gli estratti sono stati saggiati sui germi elencati nella Tabella 1, col risultato a fianco di ognuno riportato e per i solventi segnati. Gli estratti con i solventi non riportati nella Tabella sono risultati in ogni caso negativi. L'estratto acquoso è stato saggiato solo su : *Staph. aureus*, *Bruc. melitensis*, *B. coli*, *My. phlei*.

TABELLA 1.

GERMI SAGGIATI.	RISULTATI.
<i>Staph. aureus</i>	± etere di petrolio.
<i>Bruc. melitensis</i>	± etere di petrolio ; acetone ; alcool etilico 96°.
<i>Bruc. suis</i>	± acetone.
<i>Bruc. abortus</i>	± etere di petrolio ; acetone.
<i>B. coli</i>	0
<i>S. typhi</i>	0
<i>S. paratyphi B</i>	0
<i>Vibrio el Tor</i>	0
<i>Microc. lysodeicticus</i>	± etere di petrolio.
<i>My. phlei</i>	+ acetone ; acqua distillata.

Sono stati preparati anche estratti con soluzione fisiologica e poi saggiati su *My. phlei*: con successive diluizioni abbiamo messo in evidenza un'attività antibatterica anche quando nel pozzetto si introduceva una quantità di estratto corrispondente a 5 centesimi del contenuto di un singolo apparato del veleno.

Per poter escludere che l'attività antibatterica messa in evidenza mediante estratti con i solventi vari, fosse dovuta ad eventuali reazioni tra solventi e sostanze presenti negli apparati del veleno, sono stati messi direttamente gli apparati velenosi sulle colture batteriche : anche queste prove hanno dato risultati positivi. Ciò dimostra che il principio antibatterico, può diffondere direttamente dagli apparati del veleno ai terreni colturali e che l'attività evidenziata mediante estratti coi solventi vari è dovuta a sostanze originariamente presenti negli apparati del veleno.

Poichè fra i diversi estratti allestiti, quello acetoneico si è dimostrato il più attivo, abbiamo studiato alcune caratteristiche fisiche del principio estratto in acetone.

Innanzitutto si è cercato di stabilire se dopo l'estrazione acetonica gli organi residui fossero esauriti per una successiva estrazione con acqua distillata. La tecnica di ricerca fu la seguente : gli apparati del veleno furono estratti con acetone per 24 ore a 25° C ; indi dopo aver allontanato l'estratto acetoneico, furono estratti con acqua distillata per 24 ore a 25° C. L'estratto acquoso venne filtrato e saggiato su *Staph. aureus*, *My. phlei*, *B. coli* e *Bruc. melitensis*. Il risultato fu positivo sulle due prime

specie batteriche e negativo sulle altre due. Ciò dimostra che con la nostra tecnica di estrazione acetonica non si esaurisce il principio antibatterico il quale può essere ulteriormente estratto con acqua distillata, a meno che non si tratti di due fattori distinti aventi differenti caratteri di solubilità.

Si è voluto quindi esaminare il limite di termoresistenza del principio antibatterico presente nell'estratto acetónico e di quello presente nell'estratto acquoso secondario dopo l'estrazione acetonica.

La tecnica di ricerca è stata la seguente : preparato un estratto acetónico risultato attivo su *Bruc. melitensis*, debolmente attivo su *My. phlei*, inattivo su *Mic. lysodeicticus*, si fece evaporare il solvente mediante circolazione d'aria a temperatura ambiente e il residuo venne diviso in 4 frazioni uguali, trattate poi come segue :

- 1) si riporta a volume iniziale con acetone;
- 2) si riscalda a 100° C per 15', indi si riporta a volume iniziale con acetone;
- 3) si riscalda a 100° C per 30', indi si riporta a volume iniziale con acetone;
- 4) si riscalda a 150° C per 15', indi si riporta a volume iniziale con acetone.

Le frazioni saggiate su colture in agar-germi diedero i risultati riportati nella Tabella 2.

TABELLA 2.

GERMI SAGGIATI.	ESTRATTO ORIGINARIO.	FRAZ. 1.	FRAZ. 2.	FRAZ. 3.	FRAZ. 4.
<i>Bruc. melitensis</i>	+	+	+	+ —	+ —
<i>My. phlei</i>	+ —	+ —	+ —	— — +	— — +
<i>Mic. lysodeicticus</i>	0	0	0	0	0

Questi risultati dimostrerebbero che il principio antibatterico presente nell'estratto acetónico resiste a 100° C per 15', ma l'attività viene notevolmente ridotta per riscaldamento a 100° C per 30' e a 150° C per 15'.

Per la ricerca del principio antibatterico estraibile con acqua distillata dopo l'estrazione acetonica è stata seguita la seguente tecnica : preparato un estratto acquoso secondario dopo l'estrazione degli apparati del veleno con acetone, esso viene in parte riscaldato a 100° C per 10', in parte a 110° C pure per 10'.

La parte riscaldata a 100° C per 10', venne divisa per centrifugazione (20' a 4 000 giri al minuto) in :

a) frazione limpida, parzialmente deproteinnizzata, molto attiva su *My. phlei* (fig. 1, I).

b) deposito contenente le proteine coagulate e precipitate, riportato con acqua distillata a volume iniziale, debolmente attivo su *My. phlei* (fig. 1, H).

Il deposito b) non è stato lavato e quindi la debole attività antibatterica potrebbe essere dovuta alla parte di a) che impregnava il deposito, oppure

ad una frazione del principio antibatterico trasportata dalla parte coagulata e precipitata.

La parte riscaldata a 110°C per $10'$ venne anch'essa divisa per centrifugazione ($10'$ a 4000 giri al minuto) in :

c) frazione limpida, parzialmente deproteinnizzata, molto attiva su *My. phlei* (fig. 2, P);

d) precipitato contenente le proteine denaturate, riportato in sospensione con acqua distillata a volume iniziale, fortemente attivo su *My. phlei* (fig. 2, O).

Anche se il prodotto d) non è stato lavato e quindi poteva trattenere una parte del principio antibatterico che era presente in c), la forte attività antibatterica su *My. phlei* ottenuta con d) non sembra riferibile a un semplice inquinamento con a), ma forse ad una parziale precipitazione del principio antibatterico, precipitazione più abbondante di quella provocata col trattamento a 100°C per $10'$.

Questi esperimenti dimostrerebbero che il principio antibatterico presente nell'estratto acquoso dopo estrazione degli apparati del veleno con acetone, resiste a 100°C per $10'$ e a 110°C pure per $10'$, e che in parte precipita in seguito al trattamento termico.

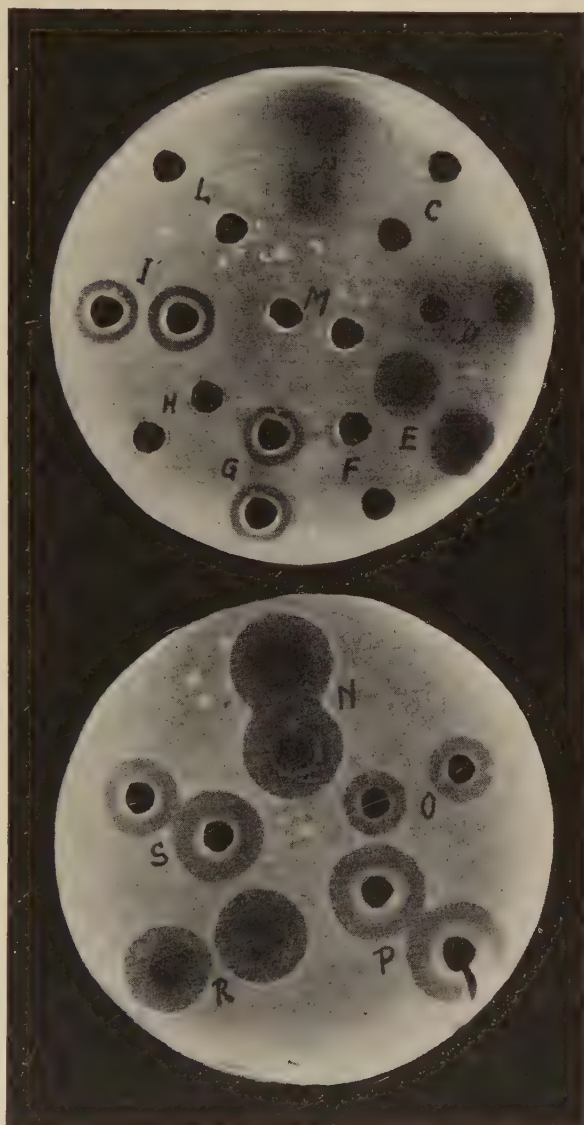


Fig. 1 et 2. — Azione del veleno d'Ape su coltura di *Mycobacterium phlei* (per la spiegazione vedere il testo).

I risultati dei trattamenti termici coi quali si è ottenuta la precipita-

zione delle proteine e la dimostrazione che in parte il principio antibatterico era presente nel precipitato, non consentono una sicura differenziazione fra questi fattori e il principio tossico *apitossina* che è ritenuto dagli Autori come un polipeptide.

La differenziazione non è stata raggiunta neppure con aggiunta di alcool etilico 96° nelle proporzioni di 1 : 1 all'estratto acquoso secondario, ottenuto dopo estrazione degli apparati velenosi con acetone.

Infatti l'estratto acquoso, addizionato di alcool etilico 96° (1 : 1) fu diviso per centrifugazione (20' a 4000 giri al minuto) in due frazioni :

fraz. e) liquida, che risultò attiva su *My. phlei* (fig. 1, G).

fraz. f) precipitato, che lavato con acqua + alcool e poi riportato in sospensione a volume iniziale con acqua + alcool risultò inattivo su *My. phlei* (fig. 1, F).

Poichè col trattamento alcoolico 1 : 1 non si ottiene la denaturazione e precipitazione di tutte le frazioni proteiche presenti in un estratto acquoso, i risultati ottenuti lasciano ancora il dubbio che la frazione tossica polipeptidica possa essere rimasta in soluzione, rimanendo perciò non differenziabile rispetto al principio antibatterico.

A completamento di queste prime ricerche sull'attività antibatterica di estratti di apparati del veleno d'Ape con solventi vari, abbiamo voluto vedere se il *fattore tossico*, estraibile con acqua dopo esaurimento degli apparati del veleno con acetone, resiste al riscaldamento a 110° C per 10' e se si trova nel precipitato contenente la proteine coagulate (sempre nella supposizione che il principio tossico *apitossina* sia un polipeptide) o se invece non precipita col riscaldamento. Queste prove furono intese come ricerca di una differenziazione tra il principio tossico ed il principio antibatterico della cui resistenza a 110° C per 10' già abbiamo avuto dimostrazione.

Preparato con la solita tecnica l'estratto acquoso secondario dopo estrazione acetonica, esso venne portato a 110° C per 10' e diviso per centrifugazione in due frazioni :

g) frazione liquida limpida;

h) precipitato che venne ripetutamente lavato e poi riportato in sospensione in acqua distillata.

Le due frazioni g) ed h) vennero iniettate per la prova di tossicità nel muscolo pettorale di passero e nel peritoneo di topo albino alle dosi corrispondenti all'estratto di 1 e di 3 apparati del veleno in considerazione che, secondo PHISALIX e altri autori, la puntura di 2-3 Api sarebbe letale per il passero.

Per ogni dose furono iniettati 2 passeri e 3 topi. L'iniezione della frazione g) è stata letale per tutti gli animali, mentre con la frazione h) è morto solo un passero ma a distanza di 20 ore dall'iniezione e senza sintomi di avvelenamento per cui si può ritenere probabile che la morte non dipenda dalla tossicità della sostanza iniettata.

Tali risultati dimostrerebbero che il principio tossico estraibile con acqua da apparati del veleno previamente estratti con acetone, resiste a

110° C per 10', non precipita con la frazione proteica denaturata a 110° C per 10' ma rimane in soluzione.

Non è stata quindi possibile una differenziazione rispetto al fattore antibatterico che pure resiste a 110° C per 10' e rimane, almeno nella maggior parte, in soluzione nella frazione liquida. Inoltre il principio tossico messo in tal modo in evidenza, non precipitando col trattamento termico a 110° C per 10', sarebbe con probabilità differenziabile dalle proteine e quindi dal principio tossico apitossina ritenuto un polipeptide. Ciò dimostrerebbe come il veleno di Ape sia complesso e ancora poco conosciuto anche nei riguardi dei suoi costituenti principali.

CONCLUSIONI RIASSUNTIVE

Nelle nostre ricerche abbiamo avuto la conferma delle proprietà antibatteriche del veleno d'Ape. Tali proprietà erano accennate genericamente in PHISALIX (1922), sono state poi segnalate da SCHMIDT-LANGE nel 1941 in un preparato farmaceutico a base di veleno d'Ape, mentre per il veleno in sé sono state segnalate da PAVAN nel 1949.

Noi abbiamo trovato che il fattore antibatterico presente nel veleno subisce variazioni quantitative notevolissime e ciò può essere messo in relazione anche con le variazioni della quantità e della costituzione del veleno riscontrate in dipendenza di fattori sia intrinseci sia ambientali.

Le proprietà antibatteriche sono state messe in evidenza con diverse tecniche e i dati trovati possono essere riassunti nei seguenti punti :

1) Il principio antibatterico è estraibile con vari solventi (acetone, acqua, soluzione fisiologica, etere di petrolio, alcool etilico).

2) Il principio antibatterico è attivo in vario grado su : *Mycobacterium phlei*, *Brucella melitensis*, *Brucella suis*, *Brucella abortus*, *Staphylococcus aureus*, *Micrococcus lysodeicticus*.

3) L'attività antibatterica non è dovuta ad eventuali reazioni tra i solventi e sostanze presenti nel veleno o a sostanze che si liberano in seguito al trattamento con i solventi, ma a sostanze originariamente presenti nelle ghiandole e nei serbatoi, poichè è evidenziabile anche applicando direttamente sulle colture microbiche le ghiandole e i serbatoi del veleno freschi e non trattati.

4) L'estrazione acetonica da noi effettuata non esaurisce il *principio antibatterico* il quale può essere ulteriormente estratto con acqua distillata. Ulteriori ricerche intese a chiarire i limiti della estraibilità con vari solventi verranno eseguite in futuro.

5) Il *principio antibatterico* presente negli estratti acetonicici resiste a 100° C per 15' ; l'attività viene notevolmente ridotta per riscaldamento a 100° C per 30' e a 150° C per 15'.

6) Il *principio antibatterico* estraibile con acqua dopo l'esaurimento dell'apparato del veleno con acetone, resiste a 100° C per 10' e rimane in soluzione.

7) Il *principio antibatterico* estraibile con acqua dopo l'esaurimento dell'apparato del veleno con acetone, resiste a 110° C per 10' e in parte precipiterebbe con questo trattamento.

8) Mediante la precipitazione alcoolica (1 : 1) delle proteine dell'estratto acquoso dopo l'esaurimento con acetone, si ottiene un precipitato inattivo, mentre il fattore antibatterico rimane in soluzione.

9) Il *principio tossico* estraibile con acqua distillata da ghiandole e serbatoi del veleno previamente esauriti con acetone resiste a 110° C per 10'; col riscaldamento non precipita con le proteine ma rimane in soluzione. Non è quindi possibile una netta differenziazione rispetto al principio antibatterico che pure resiste a 110° C per 10' e permane, almeno nella maggior parte, in soluzione. Inoltre il principio tossico messo in tal modo in evidenza, non precipitando col trattamento termico a 110° C per 10', sarebbe con probabilità differenziabile dai polipeptidi ai quali secondo vari Autori appartarrebbe il principio tossico detto *apitossina*; ciò lascia supporre che i *fattori tossici* siano molteplici e almeno in parte essi siano differenziabili dal *principio antibatterico*.

10) Si ottiene un alone su coltura di *Mycobacterium phlei* in agar-germi anche con una quantità di estratto corrispondente a 5 centesimi del veleno grezzo di un'operaia. Un apparato del veleno può contenere 0,2-0,4 milligrammi di veleno grezzo e pertanto se questo fosse costituito dal solo fattore antibatterico, la inibizione sarebbe dovuta a milligrammi 0,01-0,02 di sostanza. Si deve però considerare che in realtà il fattore antibatterico è solo uno dei costituenti del veleno grezzo che risulta costituito da numerose sostanze differenti diluite in un mezzo liquido.

Ciò mette ancor più in evidenza l'interesse che può avere lo studio delle proprietà antibatteriche del veleno d'Ape.

Dal punto di vista della conoscenza chimica del veleno d'Ape, i dati che si possiedono sono del tutto preliminari e insufficienti a trarre qualsiasi conclusione. Pertanto questa è una ricerca che sarà ampliata ed approfondita in futuro.

Per ora possiamo constatare come l'esistenza del fattore antibatterico nel veleno d'Ape richiami fatti analoghi noti per altri secreti animali e in particolare anche per secreti di insetti dell'ordine degli Imenotteri.

Senza voler estendere ora il paragone ai secreti di vertebrati velenosi (ad esempio Rettili e Anfibi) che accanto a proprietà tossiche generali hanno anche attività antibatterica, e limitandoci ai dati che si possiedono per gli Insetti, dobbiamo rilevare come finora solo tre fattori antibatterici sono stati isolati allo stato puro e riconosciuti chimicamente e cioè l'acido formico dei *Formicinæ*, la iridomirmecina di *Iridomyrmex humilis* Mayr. (*Formicidæ Dolichoderinæ*) e l'aldeide salicilica della larva del Coleottero *Melasoma populi* L. (PAVAN, 1948, ecc.). Per ora possiamo dire soltanto che il fattore antibatterico di *Apis mellifica* L. è sicuramente differenziabile da tutti e tre questi prodotti.

L'origine del fattore antibatterico del veleno d'Ape ci pare di poterla sicuramente riferire alle ghiandole del veleno, senza che si possa per ora

scendere in maggiori dettagli. La sua funzione nella biologia dell'animale non è nota mancando qualsiasi dato in proposito. Pensiamo però che possa trattarsi di una proprietà accessoria che non trova giustificazione nei particolari fini cui è adibito il veleno, come del resto non si comprende finora quale significato per la biologia dell'animale possano avere le proprietà antibatteriche dell'acido formico, della iridomirmecina e dell'aldeide salicilica nei casi sopraricordati, dove la funzione biologica ben riconoscibile di questi tre prodotti è invece quella insetticida.

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QUELQUES RÉGULATIONS SOCIALES DANS LA CONSTRUCTION CHEZ LES ABEILLES

par Roger DARCHEN

Si les nombreux problèmes évoqués par le travail des Abeilles ont, de tous temps, intéressé les hommes, l'on ne peut guère, malheureusement, en trouver d'études systématiques jusqu'à nos jours. Citons RÉAUMUR proposant au mathématicien KÆNIG le problème des dimensions des fonds des cellules de cire, et les admirables observations de HUBER en 1814, décrites dans les *Observations sur les Abeilles*.

Encore faut-il à ce propos faire les remarques suivantes : tous les auteurs se sont principalement arrêtés : 1^o plus aux formes des cellules qu'aux rayons eux-mêmes ; 2^o plus à des descriptions qu'à des recherches expérimentales.

Ce qui intrigue RÉAUMUR, c'est de savoir comment les Abeilles vont incliner les losanges des fonds des cellules pour épargner la cire et emmagasiner le maximum de miel. Ce qui éveille l'attention de HUBER, c'est surtout l'évolution des cellules d'un rayon. Il évoque cependant le parallélisme des rayons, le raccordement des cellules mâles et femelles, l'irrégularité des cellules... Il pose volontairement plus de questions qu'il n'en résout. Il dit ainsi : « Comment les Abeilles prennent-elles de si justes mesures, et connaissent-elles la direction parallèle à celle du premier rayon ? Comment ces Insectes peuvent-ils se tirer d'un pas aussi difficile (passer des cellules mâles aux cellules femelles et inversement) ? » Il nous montre des doutes : « Mais, si cependant quelque chose dans la conduite des Abeilles pouvait donner l'idée d'un consentement presque unanime (ce que nous ne présentons que comme une apparence très douteuse)... »

Matériel et méthode.

D'ailleurs, la méthode employée par HUBER ne pouvait guère l'emmener bien loin dans ses observations. Pourquoi ? Parce que l'étude directe d'une ruche au travail est un problème extrêmement complexe : les Abeilles cirières ne travaillent presque exclusivement qu'en grappe qui cache les travailleuses à l'observateur. Je dirais même que sa technique pour obvier à cet inconvénient devait obligatoirement l'amener à faire des observations partielles et même des erreurs. Nous savons en effet que les Abeilles de cet auteur travaillaient à rebours, c'est-à-dire de bas en haut. Les cirières au travail étaient ainsi toujours visibles. Mais, au moyen de

cette technique, ne s'interdisait-il pas de découvrir le rôle des Abeilles entourant les travailleuses, si elles en avaient un ? HUBER ne croit pas à ce rôle parce que, dans la construction des cellules d'un rayon, il s'agit « d'opérations partielles, successives, où chaque Abeille semble agir individuellement dans une direction imprimée par l'état dans lequel se trouve l'ouvrage qu'elle est appelée à continuer ».

Avouons qu'à HUBER, malgré sa prise de position, est souvent bien gêné par des problèmes comme le raccordement des cellules mâles et femelles et qu'il est ébranlé dans une position où l'ont amené ses expériences.

Une autre méthode de recherche était donc nécessaire. Il fallait, d'une part, laisser aux Abeilles la faculté de construire leurs rayons le plus naturellement possible et, d'autre part, provoquer quelques perturbations expérimentales pour observer leur façon d'y réagir. Je devais encore choisir les perturbations les plus simples possible, afin de permettre une interprétation facile.

Par suite, la plupart des expériences qui vont être décrites dans ce travail se référeront à cette méthode générale qui consiste à rapprocher ou à écarter anormalement des rayons et, simultanément, de couvrir ou non les rayons voisins avec une paroi quelconque de grillage, de rhodoïd ou de carton.

Je compléterai cette technique par celle qui consiste à pratiquer des brèches dans des rayons construits et à étudier leurs réparations.

Quelques ruches ordinaires, les matériaux ci-dessus, quelques morceaux de cire gaufrée, voilà tout le matériel nécessaire pour mes travaux.

La pose des assises des rayons. Les retouches.

Avant de m'indiquer le genre d'expériences à effectuer, l'observation des phénomènes naturels à l'intérieur d'une ruche va me donner la possibilité de faire quelques constatations intéressantes.

D'abord l'apiculteur débutant ne tarde guère à apprendre à ses dépens que ses ruches sont régies par certaines lois immuables : rapproche-t-il trop deux rayons, ils ne tardent pas à être réunis au grand dam de l'intérêt de ses ruches à cadres mobiles ; l'un des cadres est-il trop près d'une paroi, le voici solidement attaché au bois de la ruche ; écarte-t-il trop ses cadres, il constate des constructions parasites dans toutes les directions.

L'examen des ruches en paille ou celui des ruches Warré dans lesquelles les Abeilles peuvent construire plus librement leurs rayons nous permet ensuite d'indiquer les points suivants : 1° les rayons ne sont pas obligatoirement rectilignes et construits parallèles à un même plan d'un bout à l'autre de la ruche ; ils peuvent être courbes ou peuvent former entre eux des angles (la figure 1 nous donne quelques croquis relevés dans ces types de ruche) ; 2° cependant, ils forment toujours des régions où le parallélisme est respecté (fig. 1).

Ces observations semblent donc nous montrer que *les Abeilles cirières*

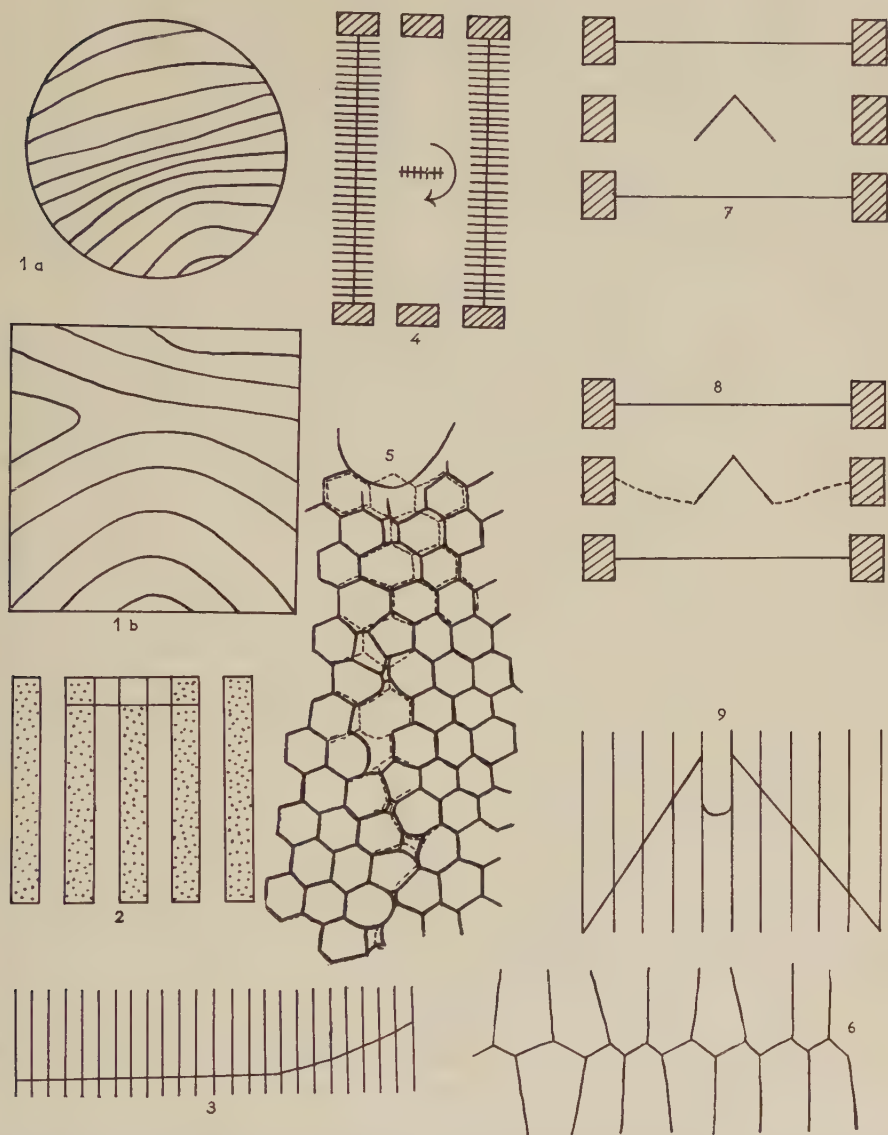


Fig. 1. Disposition des rayons dans un panier et une ruche Warré (ruches sans cadres). — Fig. 2. Les Abeilles disposent d'une façon irrégulière de nouveaux rayons sur une large assise horizontale en bois, située entre deux cadres construits. — Fig. 3. Profondeur des cellules élevées sur une lame de cire courbe. Le parallélisme entre les rayons voisins est rétabli par une variation régulière de la profondeur des cellules. — Fig. 4. Lame de cire fixée perpendiculairement au rayon. La flèche indique le sens dans lequel elle sera tordue au cours de l'étirage qui rétablira le parallélisme. — Fig. 5. Retouches des alvéoles dans la deuxième phase de la construction ; en trait plein, première phase ; les cellules de la seconde phase en pointillé. — Fig. 6. Disposition irrégulière des parois des alvéoles, vues en coupes, après des retouches. — Fig. 7, 8, 9. On introduit au milieu de deux rayons une plaque de cire formant dièdre. Les Abeilles la raccordent des deux côtés (8) puis remanient la profondeur des cellules (9) pour rétablir le parallélisme des faces des rayons. Noter que le fond de la cellule correspondant à l'arête du dièdre a été remanié et déplacé.

travaillent, au moins au début, par groupes indépendants en différents points de la ruche et qu'elles obéissent tout de même à des stimuli les amenant à rendre leurs rayons parallèles.

Un examen plus minutieux de la pose des assises de cire nous fait entrer davantage dans la technique de construction des rayons chez les Abeilles. A cet effet, dans une ruche à cadres construits, j'ai remplacé plusieurs fois l'un des cadres du milieu par un autre ne possédant aucun morceau de cire gaufrée. J'ai même élargi la barre transversale du sommet de façon qu'elle touche les cadres voisins (fig. 2).

Il s'en est suivi les faits ci-dessous : 1° deux ou plusieurs assises peuvent être fixées simultanément (photo 2) ; 2° les assises sont souvent posées quelques millimètres trop près ou trop loin du rayon voisin ; 3° les constructions nouvelles ne sont pas obligatoirement dans des plans parallèles aux plans voisins. Dans certains cas, j'ai même vu des constructions de plans perpendiculaires aux plans voisins. Je trouve ici une confirmation de ce que je viens de dire sur l'existence d'équipes d'Abeilles cirières apparemment indépendantes.

Ces faits contredisent donc les affirmations de HUBER : « L'expérience nous apprend qu'on ne voit point les Abeilles commencer ça et là différents blocs de cire en même temps. Une seule ouvrière place les matériaux dans une direction qui lui paraît convenable ; elle part, une autre la remplace, le bloc s'élève, les Abeilles sculptent alternativement sur les deux faces ; mais à peine quelques rangs de cellules sont-ils construits qu'on aperçoit deux autres blocs semblables au premier établis à une égale distance et dans une direction parallèle à la sienne, l'un vis-à-vis de sa face antérieure, l'autre de sa face postérieure... »

Mais comment expliquer alors l'ordre qui existe malgré tout dans les ruches ? Les constatations suivantes vont en rendre compte : 1° les rayons qui vont s'attacher aux assises placées trop près ou trop loin subiront une courbure de façon à être bientôt placés à la distance « standard » entre chaque cadre. A la fin de la construction de tout le rayon, la courbure disparaîtra, cachée par les parois des cellules élevées de façon que toutes leurs ouvertures soient dans un même plan (fig. 3) ; 2° les rayons fixés aux assises dont les plans forment des angles plus ou moins grands avec les gâteaux voisins vont subir une torsion au cours de leur construction de façon à être eux aussi dans un plan parallèle aux rayons voisins (fig. 4 et photo 2). Cependant, *cette retouche disparaîtra bientôt* au cours de la construction parce que les Abeilles sculpteront à nouveau la cire pour rendre les cellules de cette région semblables à leurs voisines.

RETOUCHES DE CELLULES. — *Ce ne sont d'ailleurs pas les seules retouches que j'ai observées.* Il y a quelque temps, en effet, j'ai taillé dans des rayons construits des brèches pour observer la manière dont elles étaient réparées. Ces expériences m'ont permis de diviser la réparation en deux phases : 1° une phase d'ébauche des cellules (surtout des cellules centrales) permettant ainsi un rapide colmatage de la brèche ; 2° une phase de perfec-

tionnement, dans laquelle les Abeilles cherchent à obtenir une plus grande régularité dans la forme des cellules. La figure 5 résume assez bien les documents photographiques qui nous livrent les deux phases de la réparation d'une brèche de 33 millimètres (photos 6 et 7). *La régularité observée est d'ailleurs obtenue plus au moyen des parois qui s'édifient que par la démolition des ébauches primitives* : une coupe dans le rayon permet de découvrir des fonds irréguliers et des parois dont les plans, loin d'être parallèles, se coupent entre eux (fig. 6).

RETOUCHES DE RAYONS CONSTRUITS ET DE PLAQUES DE CIRE GAUFRÉE. —

Mais quel sera le comportement des Abeilles cirières lorsqu'elles vont être obligées de se servir d'un substrat imposé ? A cet effet, j'ai introduit au milieu de la ruche deux plaques de cire gaufrée formant un angle (fig. 7). Les Abeilles ont, d'une part, allongé les parois des cellules de façon que les ouvertures se trouvent à peu près dans un même plan. Elles ont, d'autre part, élargi le rayon ainsi formé de manière à retrouver le parallélisme avec les rayons voisins (fig. 8). *Elles ne se sont donc occupées que du plan où se trouve le bord des cellules et non pas de leur profondeur.* Celle-ci ne paraît donc pas être sujette à une régulation ou ne l'est que dans des cas exceptionnels : les cellules de l'arête de l'angle dièdre précédemment formé étaient creusées pour établir une profondeur normale (fig. 9). Comme toujours, la régularité des formes des cellules était obtenue par les parois.

A l'appui des constatations signalées, je dispose d'autres résultats. Ici, j'ai déplacé deux parties de rayon construit l'une par rapport à l'autre dans le sens horizontal (fig. 10). Les lèvres ont été soudées à nouveau sans déplacement, et les parois ont été allongées pour que les bords des cellules de chaque face soient sur le même plan (fig. 11). On obtenait ainsi des cellules anormalement profondes.

Quelques expériences nous donneront encore l'ampleur des remaniements des rayons de cire anormalement placés. La première consiste à col-

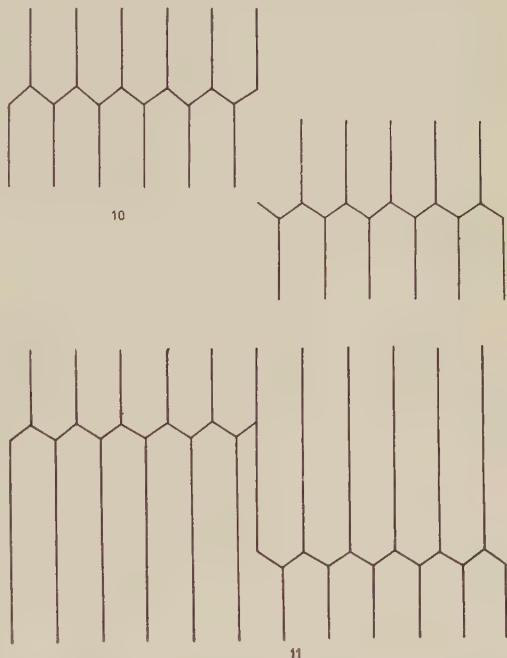


Fig. 10, 11. — Deux portions de rayons sont décalées dans le sens horizontal. Les Abeilles les raccordent (en 11) et rétablissent le parallélisme en faisant varier la profondeur des cellules.

ler un morceau de rayon construit dans un plan vertical perpendiculaire au plan du cadre déjà construit en dessous (fig. 13). Pendant un certain temps, la construction de bas en haut a semblé bloquée (je n'ai d'ailleurs pas pu voir la fin de ce travail après plusieurs mois). Il a fallu que le morceau de cire du dessus soit travaillé, sculpté à nouveau pour que le travail se poursuive lentement. La photographie présente à peu près le dernier stade que j'ai pu saisir (photo 1).

Dans la deuxième expérience, j'ai fixé un autre morceau de cire construit dans un plan horizontal perpendiculaire au plan du rayon déjà construit en dessous (fig. 12). La photographie ci-jointe nous donne encore presque la phase finale de la construction : les ouvertures des cellules ont été transférées sur les côtés (photo 3).

A ce point de notre exposé, nous pouvons formuler cette règle de la construction : *les Abeilles retouchent les cellules ou les rayons pour maintenir la plus grande régularité possible de la forme des cellules et le parallélisme des rayons.*

Le parallélisme et l'équidistance des rayons.

Il paraît intéressant maintenant de savoir comment s'opère la régulation observée, le parallélisme des rayons, et quels sont les stimuli entrant en jeu dans ce phénomène.

J'ai donc introduit à l'intérieur d'une ruche, entre deux rayons, un cadre portant une lame de cire gaufrée légèrement décalée par rapport au plan médian (fig. 14). Les Abeilles l'étirent en le ramenant dans ce plan (fig. 15).

J'ai repoussé le rayon ainsi construit pour qu'il reprenne sa position verticale trop proche du rayon voisin. Les Abeilles n'arrivent plus à l'écarter à nouveau : *la régulation ne s'opère donc que pendant la construction et non par traction sur des rayons déjà construits.*

On peut se demander encore *par quel côté se fait la régulation* puisqu'une dissymétrie est créée dans les expériences précédentes. Est-ce la distance anormalement grande entre deux rayons voisins ou la distance anormalement petite qui entraîne la régulation ? En rapprochant ou en écartant ces rayons, il est évident que *seule la présence d'un rayon anormalement proche amène la déviation en sens opposé*, alors qu'au delà de l'écart normal les variations de la distance du rayon le plus éloigné n'ont aucune influence.

Notons pour terminer que, lorsque de chaque côté du rayon en construction manque le rayon immédiatement voisin, la régulation n'existe plus.

Cependant, les apiculteurs citent un phénomène curieux s'effectuant au moment des miellées : l'allongement des cellules des hausses dont les cadres sont intentionnellement à plus grande distance que la normale.

J'ai retrouvé les mêmes résultats dans l'expérience précédente pour la partie supérieure de la languette de cire qui restait fixée dans sa position primitive. La photographie nous donne une coupe transversale effectuée dans cette région : les petites cellules se trouvent du côté du rayon anormale-

ment proche (photo 4). Qui mieux est : les cellules du rayon voisin le plus éloigné de la lame de cire gaufrée subirent à leur tour un allongement anormal, que la photographie nous met en lumière (photo 5).

De ces faits, nous pouvons déduire cette règle : si c'est nécessaire, les Abeilles établissent normalement le parallélisme par retouches successives du plan des rayons, sauf dans les cas où un substrat immuable leur est imposé. Ce sont alors les *parois des cellules qui leur servent à rétablir la distance « standard » entre les rayons*.

D'autres expériences vont maintenant nous fournir la réponse à cette question : *est-ce la présence d'une paroi de cire ou d'une paroi d'Abeilles qui induit la courbure des rayons anormalement fixés ?*

On doit répondre, semble-t-il, que c'est la cire, car, si l'on recouvre d'un carton oud'une matière plastique transparente la face du rayon le plus rapproché de la cire en construction, la courbure se forme vers eux, et non dans le sens opposé (fig. 16). Le carton est très

rapidement déchiqueté. En revanche, ces mêmes matériaux collés au rayon le plus éloigné n'inversent pas la régulation normale (fig. 17). Un manteau d'Abeilles se trouve comme d'habitude sur le rayon le plus voisin (ici, le carton et le rhodoid).

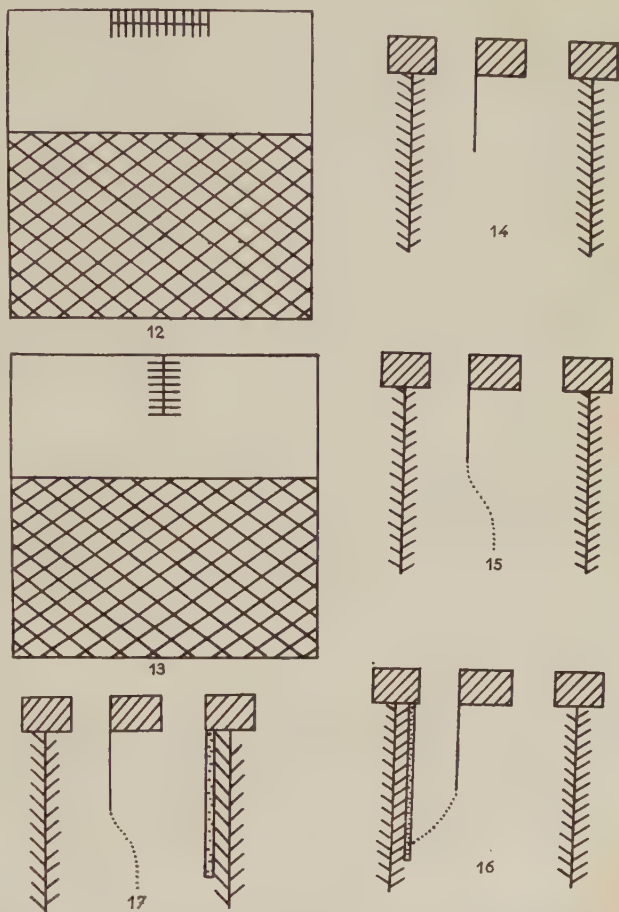


Fig. 12, 13. — Portions de rayons fixés dans un plan vertical (12) et horizontal (13) au-dessus d'un rayon déjà construit. Voir photos correspondantes. — Fig. 14, 15, 16, 17. On fixe entre deux rayons une lame de cire anormalement rapprochée de l'un d'eux (14). Les Abeilles la ramènent dans le plan médian (15), de façon à rétablir l'écartement normal (15). Mais, si le rayon le plus rapproché est recouvert de carton, la lame de cire est au contraire rapprochée et collée au carton (16). Si le carton est appliqué sur le rayon le plus éloigné, la cire est ramenée dans le plan médian comme en 15 (17).

Cependant, si je recouvre de cire l'écran interposé entre le rayon en construction et le rayon le plus voisin, je n'obtiens pas la régulation escomptée. *Serait-ce la cire façonnée en cellules qui est à l'origine du parallélisme des rayons ?*

Deux expériences cruciales confirmèrent cette opinion : 1° la simple présence d'une fenêtre d'un centimètre carré dans le carton ou le rhodoïd induisait la courbure normale ; 2° le remplacement de ces matériaux par un large écran de toile métallique, ayant à peu près les dimensions du cadre, donnait la régulation normale.

Si la cire façonnée en cellules est à l'origine du parallélisme des rayons, *il nous est facile maintenant de déterminer les stimuli entrant en action dans ce phénomène.*

Les stimuli visuels sont à éliminer, puisque la ruche est obscure. Il en est de même des ultra-sonores, provenant d'un écho hypothétique produit sur la cire, puisque celle-ci est recouverte d'Abeilles sans cesse en mouvement. Les stimuli olfactifs ne doivent certainement pas entrer en ligne de compte après l'expérience de l'écran enduit de cire. D'ailleurs, même sans ces résultats, leur rôle n'est guère pensable. *Restent donc les stimuli tactiles.*

Enfin, si on sait qu'une Abeille en train de travailler sur un rayon est trop petite pour atteindre avec l'un de ses appendices le rayon voisin trop rapproché, le problème se complique immédiatement. Les travailleuses vont-elles prendre des repères à chaque fois qu'elles construisent ? Descendent-elles le long du rayon pour contourner le grand écran métallique ? Disons tout au moins que ce serait surprenant.

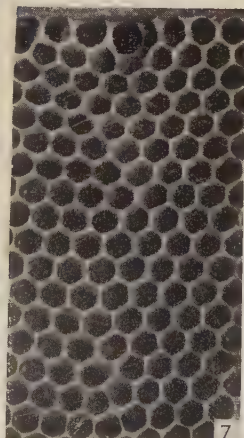
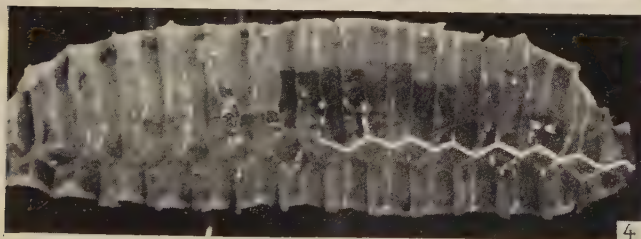
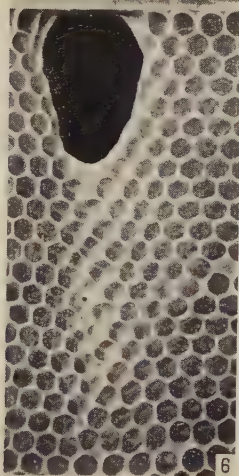
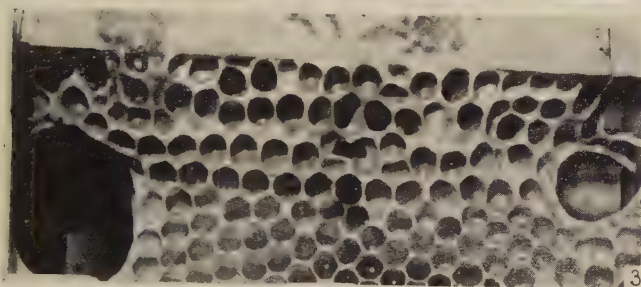
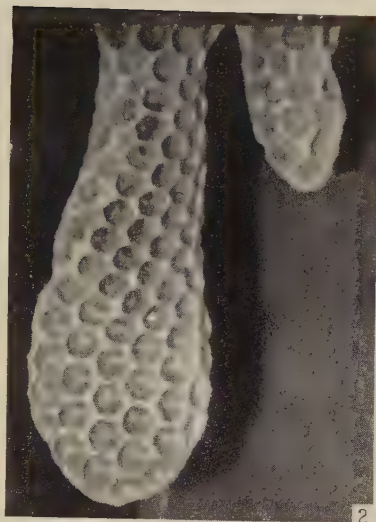
On voit donc déjà se dessiner l'hypothèse de constructions sociales dans lesquelles les bâtisseuses se trouvent sans cesse en contact avec les gâteaux voisins au moyen de la chaîne cirière. Celle-ci serait donc le canal par lequel s'écoulent les stimuli qui induisent l'écartement « standard », stimuli prenant leur source dans la cire façonnée en cellules.

Résumé.

L'étude de la construction des rayons de cire chez l'Abeille m'a permis de dégager un certain nombre de faits importants :

1° L'existence d'équipes d'Abeilles cirières travaillant, au moins au début, par groupes indépendants en différents points de la ruche. Ceci a été mis en évidence par la présence de rayons qui ne sont pas uniformément parallèles d'un bout à l'autre de la ruche, par la pose d'assises de cire dans des plans formant des angles avec les plans voisins ;

2° L'existence de modifications successives dans les cellules et les rayons de cire de façon à maintenir la plus grande régularité possible de la forme des cellules et le parallélisme des rayons. Si c'est nécessaire, les rayons en construction seront courbés, d'autres verront leur plan pivoter de 90° ; les rayons construits seront sculptés à nouveau pour que les lèvres de leurs cellules soient parallèles aux voisines ; les cellules à fonds irréguliers,



Pour l'explication des photographies, voir le texte.

par suite de brèches ou de raccords de rayons, auront des parois édifiées de façon à obtenir les ouvertures les plus égales et les plus régulières possible ;

3° Les Abeilles s'occupent plus du plan où se trouve le bord des cellules que de leur profondeur pour établir la distance « standard » entre les rayons ;

4° L'action de stimuli tactiles, prenant leur origine dans la cire façonnée en cellules et se transmettant à travers la chaîne cirière du côté des rayons anormalement proches, afin de maintenir le parallélisme et l'équidistance des rayons.

Zusammenfassung.

Beobachtungen über die Bautätigkeit der Honigbiene haben folgende wichtige Tatsachen zum Vorschein gebracht:

Es bestehen Arbeiterschaften Wachsanscheidender Bienen die, wenigstens am Anfang des Baues, gruppenweise, unabhängig von einander und in verschiedener Punkten des Bienenstockes bauen. Dieses wurde dadurch bewiesen daß die Waben, im Freibau, selten parallel laufen und daß die Arbeitsbienen wachsschichten in verschiedenen Richtungen liegen.

Es bestehe ununterbrochene Veränderungen in der Gestaltung der Zellen und der Waben, damit die größte Regelmäßigkeit in der Form der Zellen und im Gleichlauf der Waben erhalten bleibt. Die im Bau stehenden Waben werden, wenn nötig, gebogen; andere Waben werden um 90° gedreht. Schon fertige Waben werden so wiedergeschnitten daß die Ränder der Zellen miteinanderparallel bleiben. Die Zellen dessen Grund durch Schnitte oder Zusammenfügen vom Waben, unregelmäßig geworden sind, werden so verarbeitet daß ihre Öffnungen so gleichmäßig und regelmäßig wie möglich bleiben.

Die Bienen richten sich viel mehr auf die äußere Fläche der Zellen als auf die Tiefe derselben um den Einheitabstand zwischen der Waben zu Halten.

Es bestehen Tastreizungen die vom dem Zellenweise verarbeiteten Wachs herkommen und sich durch die Kette der Wachscheidenden Bienen bis zu den zu nahen Waben verbreiten um den Gleichlauf und den Gleichabstand der Waben zu erhalten.

Summary.

Some important facts are pointed out by this study of comb building.

In the beginning of the work, at least, the bees are performing apparently independent work. In the Hives, the combs are not always parallel from side to side; the foundation plane can be perpendicular to the neighbour ones.

After-touches are often observed; they provide a better shape to the cells, to the equidistance and parallelism of combs. If it is possible and necessary, the workers will curve and turn the combs; or, once more, they rebuilt partially the combs to obtain parallelism of the edges of the cells.

The edges of the cells more than their depth, are used to settle the standard distance between combs.

Worked and too nearly founded waxseems to be the source of the tactile stimuli conveyed through the chain of the wax workers to get the equidistance and parallelism of the combs.

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UNTERSUCHUNGEN ZUR KASTENDETERMINATION IN DER GATTUNG *FORMICA*

3. DIE KASTENDETERMINATION VON *FORMICA RUFA RUFO-PRATENSIS MINOR* Gößw.

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1. EINLEITUNG UND PROBLEMSTELLUNG

Bekanntlich bestehen über die Kastendetermination der Ameisen seit FOREL's und EMERY's Zeiten zwei gegensätzliche Anschauungen: blastogene oder trophogene Ausprägung des weiblichen Dimorphismus. Der auf WEISMANN zurückgehende Ausdruck „blastogen“ wurde in neuerer Zeit derartig verschieden ausgelegt, daß vorgeschlagen wurde, ihn künftig nicht mehr zu verwenden (LIGHT, 1942-1943). Für manche Autoren ist dieser Terminus identisch mit „genetisch“. Nach unserer Ansicht wäre eine Kastendetermination dann genetisch, wenn sie durch differentielle Germariummitosen (die mit verschiedenen Genbestand heranwachsende Oocyten zur Folge haben müßten) oder andere chromosomale Vorgänge z. B. während der Meiose oder Befruchtung zustande käme. Dafür haben sich aber bisher keinerlei Anhaltspunkte ergeben (1).

Der Gegensatz zur genetischen Kastendetermination ist die Kastendetermination als Modifikation, die trophogen durch die Ernährung der Larven oder blastogen durch die Versorgung der Oocyten zustande kommen kann. Wir fassen unter dem Ausdruck „blastogen“ alle Faktoren der Kastendetermination zusammen, die bis zur Ablage auf die Eizelle einwirken, sofern sie nicht von im Kern (oder Cytoplasma) der Eizelle lokalisierten Genen ausgehen.

Bei der Kastendetermination von *Formica rufa rufo-partensis minor* Gößw., der Kleinen Roten Waldameise, im Folgenden als KRW bezeichnet, konnte in den vorangegangenen Untersuchungen das Vorhandensein sowohl von blastogenen wie auch trophogenen Faktoren nachgewiesen werden. Das Ziel dieser Untersuchungen war es nun, die beiden Einflüsse in ihrer Wirksamkeit durch Aufzuchten mit ♀ der eigenen Art gegeneinander abzugrenzen. Die Fragestellung lautet also nicht, sind die

(1) Die von KERR (1950 a) entwickelte Vorstellung über die genetische Kastendetermination der Meliponinen ist rein formal und wird überdies durch die leichte Verschiebbarkeit des Kastenverhältnisses durch Umweltseinflüsse in Frage gestellt.

Kasten blastogen oder trophogen bedingt, sondern in welchem Umfang sind die beiden Faktoren wirksam.

2. VORANGEGANGENE UNTERSUCHUNGEN

a. Der Saisondiphormismus der Oogenese bei der Kleinen Roten Waldameise.

Bei einer den Jahreszyklus erfassenden Bearbeitung der Oogenese der KRW ergab sich ein Saisondiphormismus der Oocyten, der mit einem unterschiedlichen Aufbau des gesamten Ovarioleninhaltes verbunden ist (BIER, 1952 a, 1954 a). Die Nährzellen und vor allem deren Kerne

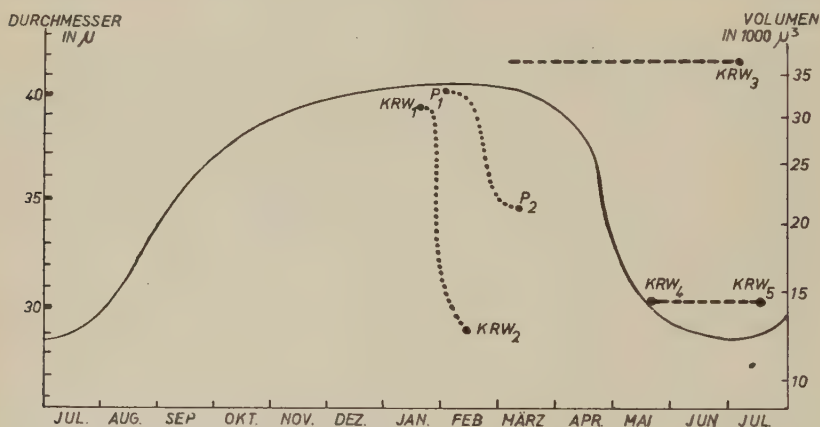


Abb. 1. — Jahresverlauf der Nährzellengröße.

— Verlauf im Freiland im Raume von Würzburg.

... Verlauf bei 27° C.

--- Verlauf bei 4 ± 1° C.

Alle Werte gemessen an der kleinen Roten Waldameise, nur P₁-P₂ an *F. r. pratensis*.

zeigen jahreszeitlich ausgeprägte Unterschiede. Der größte erreichte Kerndurchmesser, gewonnen aus je 30-50 Einzelmessungen an 26 Eierstöcken, ist in seinem Jahresverlauf in Abb. 1 dargestellt. Das zu bestimmten Zeiten gesteigerte Nährzellkernvolumen wird in mit der Kerngröße zunehmenden Maße von weiteren Anzeichen erhöhter Ribonukleinsäure- und Eiweißsynthese begleitet: Vergrößerung der Nukleolen und Ausbildung einer stark basophilen Kernmembran. In der Oocyte selbst wirkt sich der Saisondiphormismus des Nährfaches so aus, daß bei großen Nährzellkernen im hinteren Pol der Eizelle große, ribonukleinsäurehaltige, dotterfreie Plasmaregionen entstehen (Abb. 2), während in den von kleinen Nährzellkernen versorgten Oocyten an der gleichen Stelle nur ein schmaler basophiler Saum gebildet wird, der oft mit dem Keimhautblastem ganz verschmolzen ist (Abb. 3).

Nachdem während der Winters die Eiablage eingestellt ist (die KRW hat auch keine überwinternde Brut) erlangen die Oocyten mit den großen Polplasmen nach Erwachen aus der Winterruhe ihre endgültige Größe und werden nach der „Sonnungsperiode“ (vergl. GößWALD, 1951 a), in der sich ♀ und ♂ auf der Nestoberfläche den wärmenden Sonnenstrahlen aussetzen, abgelegt. Nach dieser Sonnungsperiode wird ein eigener Wärme haushalt in den aus organischem Nestmaterial bestehenden Nestkuppeln aufrechterhalten (STEINER, 1947) und dieser Zeitpunkt wird auch in der Jahreskurve der Nährzellkerngröße durch den scharfen Abfall der Kernvolumina angezeigt. Aus den ersten Aufzuchten entstehen in der Regel Geschlechtstiere, darauf den ganzen Sommer über nur ♂ (GößWALD, 1951 b).



Abb. 2. — Oocyte mit Winterpolplasma. Fixiert am 6.2 nach Helly. Färbung Gallocyenin. Fle = Follikel-epithel, Plp = Polplasma (aus Bier 1952 a).

Die Ablage der ersten Eier nach der Ueberwinterung wird durch fortgesetzte Kälteeinwirkung bis in den Sommer hinein verzögert. Bei dieser Behandlung bleibt die winterliche Nährzellengröße erhalten (Abb. 1, KRW₃). Bringt man die Königinnen dann in einen Warmraum von 27° C, so beginnen sie innerhalb einiger Tage mit dem Eierlegen. Zur Ablage der Wintereier ist die Pflege der ♀ durch eine größere Anzahl von ♂ nicht erforderlich, während die danach einzetzende Produktion des 2. Eityps, der sog. Sommereier, nur dann stattfindet, wenn die Königinnen durch eine größere Anzahl von Pflegerinnen versorgt werden. Dieser biologische Befund deckt sich mit dem zytologischen, daß die zuerst abgelegten Eier aus überwinterten

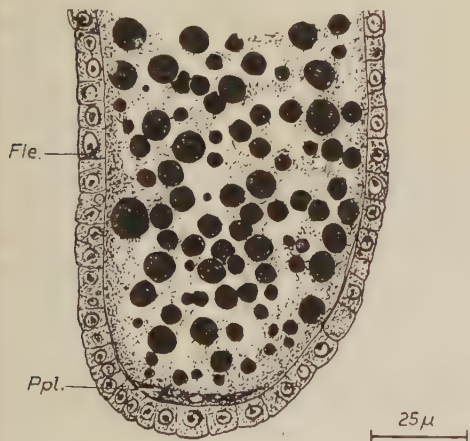


Abb. 3. — Oocyte mit Sommerplasma. Fixiert am 3.7 wie Abb. 2.

Oocyten und noch während des Herbstes gespeicherten Aufbaustoffen stammen.

Dieser Eityp mit großem Polplasma wird deshalb von jetzt ab Winter-

Ei (w-Ei) genannt, während das im Sommer laufend produzierte Ei mit kleinem Polplasma als Sommer-Ei (s-Ei) bezeichnet wird.

Schließlich ergaben zytologische Untersuchungen wie auch die Messung und Wägung der Eier und die noch später zu besprechenden Aufzuchtversuche, daß es auch im Winter möglich ist, s-Eier zu gewinnen. Bringt man nämlich weit vor dem Zeitpunkt der ersten Eiablage, im Dezember oder einem der folgenden Monate, ausgegrabene ♀ zu dieser Zeit in den Warmraum, so beginnen sie nach der Ablage ihrer w-Eier mit der Produktion der s-Eier (vergl. Abb. 1 KRW₁-KRW₂). Es ist somit möglich vom Dezember an, wenn die Nährzellen ihre maximale Größenklasse erreicht haben, bis in den Hochsommer (Juli) w- und s-Eier für experimentelle Zwecke gleichzeitig zur Verfügung zu haben.

In Abb. 1 sind auch die Nährzellkerngrößen nach experimenteller Temperatureinwirkung eingetragen, die Befunde an *Formica rufa pratensis* Retz. (P₁-P₂) sind zum späteren Vergleich wichtig. Daß die Nährzellkerngröße keine reine Funktion der Temperatur ist, zeigen die Kerngrößen der ♀, die nach Ablage ihrer w-Eier in den Eisschrank verbracht wurden und trotz eines über 2 Monate dauernden Aufenthaltes bei 4° C keine ansteigende Tendenz der Nährzellkernvolumina erkennen lassen (KRW₄-KRW₅).

b. Nachweis eines Jahreszyklus der trophischen Tendenzen bei den Arbeiterinnen der Wiesenameise.

Die Wiesenameise *Formica rufa pratensis* Retz. zieht im Gegensatz zur KRW im Raume von Würzburg im Jahre zwei Geschlechtstiergelege heran, und zwar unmittelbar nach dem Erwachen aus der Winterruhe reine Geschlechtstierbruten, danach ♀ und im Juli-August nochmals Geschlechtstiere, aber diesmal gemischt mit Arbeiterbrut. Darauf werden bis zum Ende der Brutsaison im Herbst nur noch Arbeiterinnen aufgezogen. Da die *pratensis*-♀ die KRW-Eier leicht adoptieren, bot sich durch Zugabe *konstanten* Eimaterials, nämlich des KRW-w-Eies, die Möglichkeit alle etwaigen blastogenen Faktoren bei der Kastendetermination auszuschneiden und zu untersuchen, ob bzw. in welchem Maße die zweimalige Aufzucht von Geschlechtstieren bei *pratensis* von trophogenen Vorgängen abhängig ist.

Arbeitergruppen, die aus einem Nest stammten, das vor der Aufzucht von Geschlechtstieren stand, zogen auch im Experiment aus dem KRW-w-Ei ♀ und solche aus den Nestern mit Arbeiterbrut aus dem gleichen Eityp nur ♀. Damit war ein Jahreszyklus der trophischen Tendenzen der *pratensis*-♀ und seine kastendeterminierende Wirkung nachgewiesen (GÖßWALD und BIER, 1953 b).

Arbeiterinnen mit der Tendenz zur Aufzucht von Geschlechtstieren werden von jetzt an als Gynen-♀ (G-♀) und solche mit Arbeiterinnenaufzuchtstendenz als Ergaten-♀ (E-♀) bezeichnet. Die Symbole werden mi

Gegensatz zu denen der beiden Eitypen (w- und s-Ei) groß geschrieben, da der trophogene Einfluß über den Eityp „dominiert“.

c. Nicht durch den Jahreszyklus bedingte trophogene Einflüsse und der Zeitpunkt der Kastendetermination.

In einer mit einer Königin in einem Formicar untergebrachten *pratensis*-Kolonie, die sich im Freiland noch in der Winterruhe befand und somit G-♀ enthielt, werden zwar aus den ersten abgelegten Eiern noch einige Geschlechtstiere gezogen, aber bald darauf entstehen nur noch ♀. Nach Entfernung der Königin entwickeln sich aber nochmals ♀, obwohl die Tendenz der ♀ zur Aufzucht von Geschlechtstieren nach Erwachen aus der Winterstarre, wenn auch langsam, so doch ständig nachläßt (GÖßWALD und BIER, 1953 b).

Die Aufzucht der Brut bei G-♀ bietet also nicht unbedingt Gewähr für die Entwicklung von Königinnen. Auch durch Verminderung der Anzahl der Pflegerinnen unter 25 entstehen bei weisellosen G-♀ aus dem unter natürlichen Bedingungen Geschlechtstierbruten liefernden w-Ei nur Arbeiterinnen.

Durch Austauschversuche aus solchen kleinen Gruppen, in denen Arbeiterinnen aufgezogen wurden, in große, in denen sich Geschlechtstiere entwickelt hätten, ließ sich der Zeitpunkt der Kastendetermination ermitteln. Die Larven sind, wenn die Zuchttemperatur 27° C beträgt, nach 72^h endgültig determiniert (1). Überträgt man sie nach diesem Zeitpunkt aus Gruppen, die weniger als 25 ♀ enthalten, in solche, die mehr als 100 ♀ zählen, so entwickeln sich trotzdem nur ♀. Die Umkehrung des Versuches gelingt nicht, weil die in großen ♀-Gruppen bereits zum Geschlechtstier determinierten Larven sich offensichtlich bei einer zu geringen Zahl von Pflegerinnen nicht weiterentwickeln können (GÖßWALD u. BIER, 1953 a).

d. « Prædisposition » und trophogene Einwirkung auf beide Eitypen.

Nur unter Ausschaltung der nachgewiesenen trophogenen Faktoren war es möglich, die Bedeutung der beiden Eitypen für die Kastendetermination zu klären. Dies wurde durch die Methode der „Parallelzuchten“ erreicht, die ebenfalls mit weisellosen *pratensis*-♀ durchgeführt wurden. Eine größere Anzahl von Arbeiterinnen wurde zu verschiedenen Jahreszeiten aus einem Nest entnommen und nach guter Durchmischung zu gleichen Teilen auf mehrere, mindestens zwei Formicare verteilt und einem davon w- und dem anderen s-Eier von KRW-♀ gleichzeitig zur Aufzucht zugegeben.

In diesen unmittelbar vergleichbaren Aufzuchten zeigten die aus s-Eiern stammenden Bruten unter den verschiedensten Bedingungen immer eine geringere Tendenz zur Entwicklung zum Geschlechtstier (BIER, 1954 a). Die Ergebnisse sind in Tabelle 1 zusammengefaßt.

(1) Auch bei *Ecophylla smaragdina* wird nach LEDOUX (1950) die Kaste im 1. Larvenstadium endgültig determiniert.

TABELLE 1.

Vergleichende Aufzuchten von w- und s-Eiern der KRW in weisellosen *pratensis*-♀-Gruppen.

Die Entwicklungsdauer rechnet von der Eiablage bis zur Puppe mit braun pigmentierten Facettenaugen; die voraussichtliche Entwicklungsdauer der zum Teil noch vorhandenen Nymphen wurde mitberechnet, sofern das Gewicht nicht auf subletale „Intercasts“ schließen ließ.

G-♀ = Arbeiterinnen, die im Freiland Geschlechtstiere aufziehen.

E-♀ = Arbeiterinnen, die im Freiland Arbeiterinnen aufziehen.

			W-EIER.		S-EIER.			
TROPHISCHE Tendenz d. ♀.	ANZAHL der ♀.	ZUCHTEM- PERATUR (C).	KASTE.	ENTWICKLUNGSDAUER in Tagen.	DURCHSCHNITTSGEWICHT (mg).	KASTE.	ENTWICKLUNGSDAUER in Tagen.	DURCHSCHNITTSGEWICHT (mg).
G-♀	> 100	27° C	♀	28	43	♀ + Intercasts (keine Verpuppung).	35	38
G-♀	> 100	18° C	♀	45	39	♀ + Intercasts (keine Verpuppung).	47	33
E-♀	> 100	27° C	♀	36	7,3	♀	36	7
G-♀	50	27° C	♀	26	40,4	♀	26	6,8
G-♀	25	27° C	♀	27	37,1	♀	26	6,3
G-♀	20	27° C	♀ + Pseudogynen.	25	6,5	—	—	—

Aus diesen Ergebnissen läßt sich folgendes ableiten:

1. Sowohl das w-Ei wie auch das s-Ei sind im Hinblick auf die weib-

lichen Kasten omnipotent. Allerdings ist die Entwicklung des s-Eis zum ♀ nur unter bestimmten, als überoptimal zu bezeichnenden Bedingungen möglich (Bei ♂ einer anderen Art!).

2. Die Larven aus s-Eiern wachsen unter vollkommen gleichen Bedingungen langsamer heran und erreichen ein geringeres Durchschnittsgewicht als solche aus w-Eiern.

3. In einem bestimmten trophischen Bereich, der noch ausreichend zur Erzeugung von ♀ aus w-Eiern ist, aber nicht mehr genügt, um aus s-Eiern Geschlechtstiere hervorgehen zu lassen (25-50 G-♀), bewirken die *blastogenen* Faktoren *allein* die alternative Ausprägung der beiden weiblichen Kasten.

4. Bei der den natürlichen Verhältnissen zuwiderlaufenden Kombination: G-♀ + s-Ei treten Zwischenformen, sog. „Intercasts“ auf, die in der Gattung *Formica* unter Freilandbedingungen noch nicht gefunden wurden.

Diese Versuche bestätigen den vermuteten Zusammenhang des Saison diphormismus der Oogenese mit der Kastendetermination. Allerdings stellten die bis zum Stadium der Dotterbildung zurück zu verfolgenden Unterschiede in den Oocyten keine *Prædetermination* dar, da zumindest im Experiment sich aus beiden Eitypen jeweils durch trophogene Einflüsse beide Kasten entwickeln konnten.

Es wurde deshalb der Ausdruck *Prædisposition* gewählt zur Kennzeichnung der Tatsache, daß das w-Ei sich leichter zum Geschlechtstier entwickelt als das s-Ei.

Überschneiden sich *Prædisposition* des Eityps und trophische Tendenz der pflegenden Arbeiterinnen, so kommt es zur Bildung von Intercasts.

Diese Zwischenformen, die in der Größenordnung den in den Zuchten entstandenen ♀ näher stehen als den ♂, bilden mit den wenigen Exemplaren, die das imaginale Stadium erreichten, in der Thoraxform und mit den Flügelstummeln, einen kontinuierlichen Uebergang zwischen den beiden weiblichen Kasten (Abb. 4). Sie erinnern z. B. an die von STUMPER (1918) bei *Formicoxenus* beschriebenen Zwischenformen, sind aber nicht mit den Pseudogynen zu verwechseln, die in unseren Experimenten unter anderen Bedingungen entstanden.

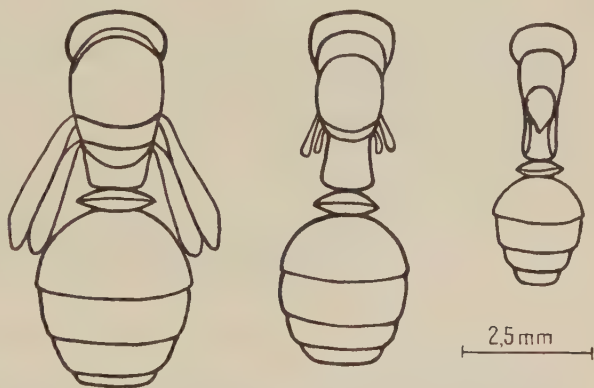


Abb. 4. — Königinnenpuppe (links), Puppe eines „Intercast“ (Mitte) und Arbeiterinnenpuppe (rechts) aus s-Eiern der kleinen Roten Waldameise mit *pratensis*-♂ im Formicar aufgezogen. Kokon, Puppenhaut und die 3 Beinpaare entfernt.

Die Intercasts sind deutlich in ihrer Entwicklung gehemmt. Es entstanden in allen Versuchen mit G-♀ + s-Eiern reichlich Nymphen, die ihrer Größe und ihrem Gewicht nach Zwischenformen erwarten ließen, aber nur in einer Zucht verpuppte sich ein Teil dieser Tiere, die Masse der Intercasts ist also subletal. Mit zunehmenden weiblichen Kastendiphormismus bilden sich offensichtlich bestimmte Reaktionsnormen aus der großen Modifikationsbreite heraus. Während die beiden Enden der Variationsbreite, Arbeiterinnen und Königinnen bevorzugt ausgebildet werden, geht die Entwicklungsmöglichkeit für die Zwischenformen vermutlich mutativ verloren. Für Betrachtungen zur Phylogenese des Kastendiphormismus erscheint es von besonderem Interesse, daß die Letalfaktoren erst am Ende der Postembryogenese, bei der Verpuppung auftreten, während die larvale Entwicklung intermediärer Formen nicht beeinträchtigt ist. Dies ist ein Anhaltspunkt, daß der vollkommene Diphormismus, phylogenetisch gesehen, eine junge Errungenschaft ist und steht in Übereinstimmung mit den Erwägungen von WILSON (1953), daß der Kastendiphormismus von den Imagines her im Laufe der Stammesgeschichte auf die Larven übergreift.

3. AUFZUCHTVERSUCHE DER BEIDEN EITYPEN MIT ARBEITERINNEN DER EIGENEN ART

a. Zuchten mit Königinnen.

Bei der Kleinen Roten Waldameise (der KRW) werden im Gegensatz zur Wiesenameise nur einmal Geschlechtstiere aufgezogen, und zwar im Frühjahr aus den ersten Gelegen (GÖßWALD, 1951 *b*), d. h. aus w-Eiern. Es sollen auch bei der KRW solche Arbeiterinnen, die zu einer Zeit aus dem Freiland eingebracht wurden, wo dort Geschlechtstiere gezogen wurden, als G-♀ bezeichnet werden und solche aus Arbeiterinnen produzierenden Nestern als E-♀.

Im Formicar entstehen aus w-Eiern bei KRW G-♀, wenn also alle Voraussetzungen zur Aufzucht von Geschlechtstieren erfüllt zu sein scheinen, in der Anwesenheit von Königinnen niemals Geschlechtstiere, sondern immer nur ♀ (siehe z.B. Tab. 2, KRW 14). Dieses Ergebnis hat sich in 1944 begonnenen, seit 1950 fortlaufend durchgeführten Aufzuchten immer wieder bestätigt. Allerdings entstanden in einem großen Teil dieser Zuchten ein zwischen 5-20 % schwankender Anteil von Pseudogynen unter den aufkommenden Arbeiterinnen.

Es war naheliegend, das Ausbleiben der Geschlechtstiere durch ein ungünstiges Verhältnis von ♀:♀ zu erklären. Unter natürlichen Bedingungen kommen im Freiland meist bei der polygynen KRW etwa 1 000 ♀ auf eine Königin. Es wurden, um dieses Verhältnis noch weiter zu unterbieten 3 500 KRW-♀ mit einer ihrer ♀ ins Formicar eingebracht,

doch lieferte die Aufzucht die gleichen Ergebnisse, nur die Durchschnittsgröße der entstehenden ♀ lag höher (Tab. 2, KRW 6). Relativ leicht gelingt dagegen die Aufzucht von *pratensis*-Geschlechtstieren neben der Königin (Tab. 2, Prat. 20 + ♀, vergl. auch GÖßWALD und BIER, 1953 b).

Es müssen im Freiland besondere Bedingungen gegeben sein, daß trotz der zahlreich im Nest vorhandenen Königinnen so große Geschlechtstierbruten aufgezogen werden. Vielleicht spielen die Temperaturverhältnisse in der Weise eine Rolle, daß die ♀ nach der Ablage der w-Eier das aus organischem Nestmaterial bestehende, durch eigenen Wärmehaushalt temperierte Nestzentrum verlassen und in tiefe Nestkammern sich zurückziehen, wodurch die ♀ während der Aufzucht der Geschlechtstiere physiologisch weisellos sind.

TABELLE 2.

ZUCHT- PROT. Nr.	VERSUCHSBEGINN.	ANZAHL u. physiolog. Zustand d. ♀+♂.	ART der und ♀+♂.	EITYP.	ENTWICKLUNGSDAUER in Tagen v. d. 1. Eiabl. bis z. 1. Verpuppung.	ERGEBNIS u. Durchschnitts- gewicht der zuerst entnommenen Brut.
KRW 14.	10-3	2 ♀ + 1 200 G-♂	KRW	w-Eier.	20	23 ♀ (9,5). 4 Pseudogynen (9,3).
KRW 6..	9-12	1 ♀ + 3 500 G-♂	KRW	w-Eier.	18	51 ♀ (14,8). 5 Pseudogynen (10,3).
Prat. 20 + ♀.	11-3	1 ♀ + 600 G-♂	Prat.	Pratens- Eier.	32	8 ♂. 1 ♀ und ♀-Larven.

b. Aufzuchten mit weisellosen Arbeitergruppen.

In kleinen weisellosen Gruppen (< 100 ♀) gelangen trotz wiederholter Versuche keine Aufzuchten und nur in einem Teil der größeren weisellosen Zuchten (> 250 ♀) entwickelte sich die Brut bis zur Verpuppung. Es wurden sämtliche 4 möglichen Kombinationen durchgetestet: w-Ei + G-♀, w-Ei + E-♀, und s-Ei + G-♀, s-Ei + E-♀, die Ergebnisse sind summarisch in Tabelle 3 dargestellt und von jeder Kombination wurde ein Beispiel in Tabelle 4 aufgenommen.

TABELLE 3.

EITYP u. Arbeiterinnentendenz (KRW-Eier, KRW- Arbeiterinnen).	ANZAHL d. Zuchten.	ANZAHL d. erfolg- reichen Zuchten.	KASTE d. entwickel- ten Tiere.	ANZAHL der Zuchten ohne aufkom- mende Brut.
w-Ei + G-♀	5	3	♀	2
w-Ei + E-♀	2	1	♀	1
s-Ei + G-♀	3	—	—	3
s-Ei + E-♀	3	2	♀	1

TABELLE 4.

PROT.- Nr.	ANZAHL d. ♀.	ANZAHL d. Eier.	VERSUCHS- DAUER.	ZUCHTERGEBNIS u. Durchschnitts- gewicht (mg.).	BEMER- KUNGEN.
KRW 12.	4 000 G-♀	400 w-Eier.	26.2-17.3	4 ♀ (42,3).	
KRW 18.	1 200 E-♀	450 w-Eier.	4.6- 5.7	Negativ.	Brut wurde bereits in frühen Lar- venstadien gefressen.
KRW 19.	1 200 E-♀	450 s-Eier.	4.6-30.6	4 ♀ (16,6). 3 Nymphen (17,3). 5 Altlarven (14,9).	
KRW 2.	400 E-♀	120 w-Eier.	26.6-8.8	12 ♀ (6,8).	Keine Pseu- dogynen.

Die Befunde aus den Formicaraufzuchten mit eignen Arbeiterinnen sind zwar wegen des hohen Anteils negativer Zuchten mit einer gewissen Unsicherheit belastet. Es tritt aber das bessere Aufkommen der Brut in den Zuchten, die die natürliche Kombinationen w-Ei + G-♀ und s-Ei + E-♀ enthalten, deutlich in Erscheinung, was nur auf eine Aufeinanderabstimmung von Eityp und Larvenernährung und Elimination nicht

„richtig“, prädeterminierter Larven durch die KRW-♀ zurückgeführt werden kann, die in den Versuchen mit *pratensis*-♀ nicht in Erscheinung trat.

Diese Ergebnisse bestätigen die Befunde mit *pratensis*-♀: Die trophische Tendenz der ♀ ist entscheidend, ob aus dem w-Ei Geschlechtstiere oder Arbeiterinnen aufgezogen werden. Die trophische Potenz der KRW-♀ ist allerdings viel geringer als die der *pratensis*-♀. Die KRW-G-♀ können aus dem s-Ei nicht mehr Geschlechtstiere ziehen.

c. Vergleich der Kastendetermination der Kleinen Roten Waldameise mit der Wiesenameise.

Ein Vergleich der Verhältnisse bei der KRW und *pratensis* erscheint besonders geeignet, die Wirksamkeit der blastogenen und trophogenen

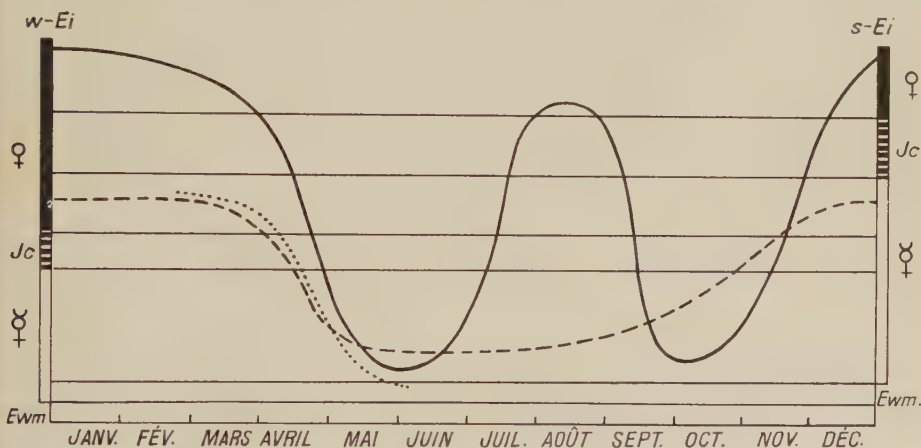


Abb. 5. — Reaktionsnorm des KRW-w-Eies (Ordinate links) und des KRW-s-Eies (Ordinate rechts) in aus dem Freiland eingebrachten weisellosen Arbeitergruppen.

— von *Formica rufa pratensis* mit mehr als 100 Arbeiterinnen.

... von *Formica rufa pratensis* mit 25 — 50 — Arbeiterinnen.

--- von *Formica rufa rufo-pratensis minor* (KRW) mit mehr als 250 Arbeiterinnen.

Jc = Intercasts.

Ewm = Entwicklungsminimum.

Faktoren bei den beiden Arten gegeneinander abzuwiegen. In Abb. 5 sind die Zuchtergebnisse in der Ordinate und der Jahresverlauf in der Abszisse eingetragen. Durch diese graphische Darstellung der kastendeterminierenden, trophischen Verhältnisse wird besonders deutlich, daß die Aufzucht von Geschlechtstieren bei der KRW nur aus w-Eiern möglich ist. Der trophische „Spiegel“ liegt in großen weisellosen KRW-G-♀-Gruppen etwa in der gleichen Höhe wie bei 25-50 *pratensis*-G-♀, für die nachgewiesen wurde, daß unter solchen Bedingungen die blastogenen Faktoren entscheidend sind und die Kastendetermination eine blastogene Modifikation ist.

Anders stellen sich die Verhältnisse bei der Wiesenameise dar. Wenn auch infolge Materialmangels (die Königinnen der vermutlich monogynen

oder höchstens oligogynen *pratensis* sind außerhalb der Sonnungsperiode praktisch unerreichbar) keine so ausgedehnte Untersuchung der Oogenese wie bei der polygynen KRW vorliegt, so geben doch die Gegenüberstellung einer zu Beginn der Sonnung und einer weiteren, nach 6 Wochen bei 27° (also unter einer Bedingung, unter der die KRW-♀ ihren minimalsten Nährzellenkerndurchmesser haben) fixierte *pratensis*-♀ den deutlichen Hinweis, daß ein Saisondiphormismus der Oogenese zwar vorhanden, aber quantitativ weniger ausgeprägt ist als bei der KRW (Tab. 5).

TABELLE 5.

	NAHRZELLENKERNDURCHMESSER in μ . $M \pm m$, $n > 30$.	
	nach Erwachen aus der Winterruhe.	nach 6 wöchigem Formi- caraufenthalt.
<i>F. rufa pratensis</i> (<i>pratensis</i>).....	$39,6 \pm 0,31$	$34,5 \pm 0,37$
<i>F. rufa rufo - pratensis minor</i> (KRW)	$38,5 \pm 0,36$	$29,0 \pm 0,24$

Nachden sich bei der KRW der Nährzellenkerndurchmesser als geeigneter Maßstab für die Ernährung der Oocyte mit Nährzellsekret, und diese wiederum als entscheidend für das morphogenetische Potential der Eizelle erwiesen hat, scheint der Analogieschluß erlaubt, daß die Eiunterschiede, das heißt die blastogenen Faktoren der Kastendetermination bei *pratensis* eine geringere Bedeutung haben als bei der Kleinen RotenWalda-meise. Auf der anderen Seite ist die trophogene Potenz der *pratensis*-♀ viel größer als die der KRW-♀. Somit spricht alles für eine trophogene Kastendetermination bei *F. r. pratensis* und eine sehr untergeordnete Rolle der blastogenen Faktoren bei dieser Art, während bei der KRW offenbar die trophogene Kastendetermination in dem Maße abgebaut wurde, in dem die blastogenen Faktoren in den Dienst der Ausprägung des weiblichen Diphormismus traten.

4. ERÖRTERUNGEN

Die Kastendetermination der KRW erwies sich als ein in den Jahreszyklus eingebettetes Gefüge blastogener und trophogener Faktoren, wobei dem blastogenen Anteil bei dieser Art das Schwergewicht zukommen dürfte.

Durch die Kombination blastogener und trophogener Einflüsse entsteht eine große Plastizität in der Aufzucht der Kasten. Wenn auch die trophische Potenz der KRW-♀ in keinem Falle zur Erzeugung von ♀ aus s-Eiern ausreichen dürfte, so wird doch von der im Experiment realisierten Möglichkeit aus w-Eiern ♀ zu ziehen zur Erhaltung geschwächter Völker im Frühjahr in gestörten Nestern sicher oft Gebrauch gemacht. Wir stimmen nur bedingt mit KERR (1950 *b*) darin überein, daß im Verlauf der Evolution mit fortschreitendem Kastendimorphismus der Zeitpunkt der Determination immer weiter vorverlegt wird. Die Anlage für eine differente Ausbildung der Kasten ließ sich in unserem Falle in die Oocyten und deren Nährzellkerne hinein verfolgen, aber der Zeitpunkt der endgültigen Determination blieb in früheren Larvenstadien erhalten. Dies muß biologisch und damit evolutionistisch als Vorteil gewertet werden.

Unbefriedigend ist, daß wir z. Zt. noch nichts Definitives über die Natur der trophogenen Faktoren aussagen können. Immerhin haben sich einige Hinweise ergeben. Der mit G und E charakterisierte Zustand der ♀ dürfte durch die Aktivität bzw. Stilllegung mit der Futtersaftproduktion in Zusammenhang stehender Drüsen bedingt sein. Vielleicht ist bei den von uns untersuchten Arten G-♀ gleichbedeutend mit aktiven Pharyngeal-und/oder Labialdrüsen, während E-♀ nur reinen Kropfinhalt verfüttern? Die Tatsache, daß die Anwesenheit von KRW-♀ auch bei Vorhandensein der entsprechenden Voraussetzungen (w-Ei + G-♀) die Aufzucht von Geschlechtstieren unterdrückt und bei den Versuchen mit *pratensis* (GÖBWALD und BIER, 1953 *b*) die Aufzucht von Geschlechtstieren bei Anwesenheit der ♀ schnell erlischt, nach Entfernung der ♀ aber wieder sofort einsetzt, spricht dafür, daß die Königin mit dem gleichen hochwertigen, vermutlich sehr eiweißreichen Futter versorgt wird, das den Larven, wenn es in entsprechenden Quanten zur Verfügung steht, die Entwicklung zum Geschlechtstier ermöglicht. Die Konkurrenz zwischen Königin und Larven um den von den Arbeiterinnen produzierten Futtersaft hat sich auch bei der Auslösung der bei den meisten Arten latent vorhandenen Arbeiterinnenfertilität gezeigt (BIER, 1954 *b*) und vor uns hat Schneirla (1953) auf die Beeinträchtigung der Königinnenfertilität durch die Brut bei den Treiberameisen aufmerksam gemacht. Ein Hinweis für das Vorkommen spezieller kastendeterminierenden Wirkstoffe wie bei der Honigbiene (ALTMANN, 1950, v. RHEIN, 1951) hat sich in unseren Versuchen nicht ergeben. Nach GÆTSCH (1937) ist die Verfütterung konzentrierter, eiweißreicher Nahrung während einer kritischen Phase auch für die Determinierung von Soldaten entscheidend. Auch die Versuche von GREGG (1942) an *Pheidole morrisi* lassen sich dahingehend interpretieren, wenn man die imaginalen Soldaten als Kostgänger der Arbeiterinnen auffaßt.

Die Verlegung des Schwergewichtes der Kastendetermination auf blastogene Faktoren scheint eine phylogenetisch junge Errungenschaft innerhalb der Gattung *Formica* zu sein, da die der KRW nahe verwandte *pratensis* nach den Aufzuchtversuchen und den cytologischen Kriterien

zu urteilen, blastogene Faktoren nur andeutungsweise besitzt. Die beschränkte Entwicklungsfähigkeit unter bestimmten Bedingungen abgelegter unbefruchteter Eier bei *Lasius* macht es aber wahrscheinlich, daß auch in dieser Camponotinen-Gattung zwei Eitypen und damit blastogene Faktoren der Kastendetermination vorhanden sind (BIER, 1952 b). Nach SCHNEIRLA und BROWN (1952) bestehen bei den Eciton-Arten die prospektiven Geschlechtstiergelege von vorn herein aus einer geringeren Anzahl von Eiern und vielleicht handelt es sich auch hier um einen zur Geschlechtstierentwicklung prädisponierten Eityp. Bei den Treibera-meisen ist die Aufzucht von Geschlechtstieren in ganz ähnlicher Weise wie bei der KRW an dem Jahreszyklus gebunden und eine Wiederholung der Geschlechtstieraufzucht in der gleichen Trockenperiode wurde auch dort nicht beobachtet, wohl aber eine Nachzucht von ♀, was eine Analogie zu unseren Beobachtungen bei der KRW darstellt.

Andererseits ist bei Arten mit geringerem Dimorphismus eine rein trophogene Kastendetermination wahrscheinlich und für *Myrmica* durch BRIAN (1952) nachgewiesen worden.

Wir möchten unsere Betrachtungen nicht schließen ohne auf die Konsequenzen einzugehen, die sich aus unseren Untersuchungen für die Kastendetermination parasitärer Ameisenarten ergeben. Es ist bei arbeitlosen Arten, wie *Anergates* und *Teleutomyrmex*, offensichtlich, daß ein den Parasiten dienliches Verhältnis der Kasten, nämlich nur Geschlechtstiere, erzeugt wird. Aber auch bei Arten, deren Arbeiterkaste, wenn auch parasitär degeneriert, noch erhalten ist, wie bei *Epimyrmica gößwaldi*, wird ein dem Parasiten und nicht dem Wirt entsprechendes Verhältnis der beiden weiblichen Kasten großgezogen, was auf blastogene Faktoren deutet (GÖßWALD, 1933). Wenn keine starre Prädetermination vorliegt, wie dies bei den arbeitlosen Parasiten zwar der Fall sein könnte, aber für Arten mit einer parasitär degenerierten Arbeiterkaste unwahrscheinlich ist, so würden die Aufzuchten der KRW-Eier bei *pratensis*-♀ ein gutes Modell für die Situation der Parasitenbrut bei der Wirtsart darstellen. Für den Parasiten ist die Arterhaltung nur von der Quote der erzeugten Geschlechtstiere abhängig. Ein Uebergang zur extrem parasitären Lebensweise dürfte deshalb erst dann möglich sein, wenn das Parasitenei zur Entwicklung zum Geschlechtstier prädisponierter ist als das Wirtsei, d. h. das Ei des Parasiten muß unter trophischen Bedingungen bereits den Weg zum Geschlechtstier einschlagen können, bei denen aus dem Wirtsei noch ♀ hervorgehen.

Zusammenfassung.

Bei *Formica rufa rufa-pratensis minor* Gößw. existiert ein Saison-diphormismus der Oogenese, der sich in einer verstärkten Nukleolenausbildung, ausgeprägteren basophilen Kernmembran und vergrößertem Nährzellkernvolumen im Winter ausdrückt. Das aus Nährzellsekret

aufgebaute Polplasma besitzt im Winter etwa das 8-fache Volumen gegenüber der Sommerform.

Durch erhöhte Temperatur wird einerseits im Winter eine typische Sommeroogenese bewirkt, andererseits durch fortgesetzte Kälteeinwirkung die Ablage der Wintereier bis in den Sommer hinein verzögert. Dadurch ist es möglich, beide Eitypen gleichzeitig für Aufzuchten zur Verfügung zu haben.

Die blastogenen Unterschiede dieser beiden Eitypen sind für die Kastendetermination bedeutungsvoll. Unter bestimmten Voraussetzungen (in einem "mittleren,, Ernährungsmilieu) entstehen allein aufgrund der blastogenen Faktoren aus Wintereiern ♀ und aus Sommereiern ♂.

Die endgültige Kastendetermination der Larven der Kleinen Roten Waldameise ist bei 27° C innerhalb von 72^h nach dem Schlüpfen aus dem Ei abgeschlossen.

Gibt man gleichstarken weisellosen Gruppen von Arbeiterinnen der Wiesenameise (*Formica rufa pratensis* Retz.) zu verschiedenen Jahreszeiten Wintereier der Kleinen Roten Waldameise zu, so ziehen sie aus diesem Eityp entsprechend ihrem Jahreszyklus abwechselnd Geschlechtstiere und Arbeiterinnen. Da der Eityp in diesen Versuchen konstant war, kann das Ergebnis nur auf einen trophogenen Zyklus der Wiesenameisen-♀ zurückgeführt werden.

Die Wiesenameisen-♀ ziehen in ihrer Geschlechtstieraufzuchtphase aus Sommereiern der Kleinen Roten Waldameise Königinnen und Intercasts.

Vergleicht man die Wiesenameise mit der Waldameise, so sind, nach den zytologischen Kriterien zu urteilen, die blastogenen Faktoren bei der ersteren Art viel geringer ausgeprägt, während ihre Arbeiterinnen bedeutend stärkere trophogene Potenzen besitzen und selbst aus dem zur Arbeiterin prädisponierten Eityp unter bestimmten Bedingungen Geschlechtstiere aufziehen.

Die Arbeiterinnen der Kleinen Roten Waldameise können dagegen aus den Sommereiern ihrer Königinnen keine ♀ mehr erzeugen, womit die Kastendetermination dieser Art faktisch auf blastogener Modifikation beruht.

Résumé.

La *Formica rufa rufo-pratensis minor* Gößw. présente un dimorphisme saisonnier de l'oogenèse, montrant un développement plus intense des nucléoles, une membrane nucléaire basophile plus marquée et un plus grand volume du noyau cellulaire nutritiel en hiver. Le volume du plasma polaire, composé de sécrétion cellulaire nutritielle, est environ huit fois plus grand en hiver qu'en été.

Une température plus élevée en hiver cause, d'une part, une oogenèse estivale typique, et un froid continu d'autre part retarde la ponte des œufs hiémaux jusqu'en été. Ainsi les deux espèces d'œufs sont disponibles pour la reproduction en même temps.

Les différences blastogéniques entre les deux espèces d'œufs ont une grande importance pour la détermination de la caste. Sous certaines circonstances (dans un milieu alimentaire « moyen ») des ♀ naissent des œufs hiémaux et des ♂ des œufs estivaux rien que par les influences blastogéniques.

La détermination de la caste définitive des larves de la petite Fourmi forestière rouge est achevée 72 heures après l'éclosion à une température de 27° C.

Si l'on donne, dans des saisons différentes, des œufs hiémaux de la petite Fourmi forestière rouge à des groupes égaux en nombre et sans reine d'ouvrières de la Fourmi des prés (*Formica rufa pratensis* Retz.), elles produisent des animaux sexués ou des ouvrières, selon leur cycle annuel à partir de ces œufs. Comme l'espèce d'œuf restait invariable dans ces expériences, le résultat ne peut être attribué qu'à un cycle trophogène des ♂ de la Fourmi des prés.

Dans leur période de production d'animaux sexués, les ♂ de la Fourmi des prés produisent des reines et des « intercastes » à partir des œufs estivaux de la petite Fourmi forestière rouge.

Si l'on compare la Fourmi des prés à la Fourmi forestière, on trouve que, à en juger par les critères cytologiques, les influences blastogéniques sont beaucoup moins marquées chez la première espèce, tandis que leurs ouvrières possèdent des facultés trophogéniques beaucoup plus fortes et produisent, dans certaines circonstances, des animaux sexués à partir de l'œuf prédisposé à produire une ouvrière.

Cependant les ouvrières de la petite Fourmi forestière rouge ne peuvent plus produire de ♀ à partir des œufs estivaux de leurs reines, ce qui prouve que la détermination des castes de cette espèce dépend, effectivement, d'une modification blastogénique.

Summary.

of the Results concerning the Caste Determination of the two *Formica* Species examined.

The *Formica rufa rufo-pratensis minor* Gößw. exhibits a seasonal dimorphism of the oogenesis, showing a more intense development of the nucleoles, a more marked basophile nuclear membrane, and a bigger volume of the nutrient-cell nucleus in winter. The polar plasm, consisting of the nutrient-cell secretion, is, in winter, eight times the volume of that in summer.

A higher temperature in winter will bring about a typical summer oogenesis, on the one hand, and continuous cold, on the other, will delay the laying of winter eggs until summer. Thus both types of eggs will be disposable for breeding at the same time.

The blastogenous differences between these two types of eggs are of great importance for the caste determination. Under certain conditions

(in a "medium" food situation), ♀ will come out of winter eggs, and ♂ out of summer eggs, merely owing to blastogenous factors.

The final caste determination of the larvae of the small red forest ant will be completed within 72 hours after leaving the egg, given a temperature of 27° C.

If equally strong groups of workers of the meadow-ant species (*Formica rufa pratensis* Retz.), without queens, are given winter eggs of the small red forest ant in various seasons, they will breed, out of this egg type sex animals or worker ants, according to their annual cycle. As the egg type was a constant one in these experiments, the result cannot but be due to a trophogenous cycle of the ♂ of the meadow ant.

In their sex-animal breeding period, the ♂ of the meadow ant will breed queen-ants and intercastes out of summer eggs of the small red forest ant.

If we compare the meadow ant with the forest ant, we see that, judging from the zytological criteria, the blastogenous factors are much less marked with the first species, whereas their workers possess considerably higher trophogenous faculties, and will breed, under certain conditions, sex animals even from the egg type predisposed to produce workers.

The workers of the small red forest ant, however, will no longer be able to breed ♀ out of the summer eggs of their queens, which proves that the caste determination of this species is, as a matter of fact, dependent on a blastogenous modification.

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A STATISTICAL ANALYSIS OF COMMUNICATION IN "APIS MELLIFERA" AND A COMPARISON WITH COMMUNICATION IN OTHER ANIMALS

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INTRODUCTION

Von FRISCH's discovery* of some of the methods by which bees communicate is of such importance that any details which can be added to his conclusions may be of value. We have therefore made a statistical analysis of some of his observations. This suggests further experiments, and poses certain questions which can reasonably be asked in research on communication between animals. We first make a historical observation. Many workers before von FRISCH had observed the dances. However the priority belongs to ARISTOTLE (*Hist. Animal.* 18, 624 b, 8). After describing the fidelity of a bee to one type of flower, he proceeds "And when they have come into the hive, they shake themselves, and three or four accompany each of them. And it is not easy to see what is being taken". The passage has been repeatedly mistranslated, but its meaning is fairly clear (KRAAK, 1953; HALDANE, 1954). The word "aposeiontai", here translated "they shake themselves", is also used by ARISTOTLE to describe the post-copulatory shaking of hens, and POLLUX used a cognate word to describe a human "danse du ventre".

Von FRISCH has described the behaviour of *A. m. carnica*. A bee which has visited a sufficiently rich source of food in the immediate neighbourhood of the hive returns and runs on the vertical comb in circles of a diameter about twice its own length. After anything from a half to two revolutions the bee turns abruptly and runs round in the opposite direction. This is the "round dance", and has no bilateral symmetry. It does not indicate the direction of the food source.

When the food source is 50 metres away, dances formed like a figure of eight are frequently seen, and the bees may wag their abdomens at the node. This wagging becomes more frequent and obvious as the source of food becomes more distant, and when this is 100 metres it can be seen in the dance of almost every bee. At distances greater than this it can be seen that the two centre parts of the "eight" over which the bee is wagging

(*) For a bibliography, and much other valuable information, we are indebted to Ribbands (1953 b).

its abdomen are straight lines. The bisector of the angle between these straight wagging parts of the path makes approximately the same angle with the vertical as the direction of the food makes with that of the sun. As the distance of the food increases, the straight parts of the dance increase in length and the angle between them decreases, until at about 600 metres the dance approximates to the human folk dance figure of straight up the centre (abdomen wagging), turn to the right, curve round, straight up the centre, turn to the left, and so on. At such distances a considerable length of the dance path, the straight run up the centre, makes the same angle with the vertical as the direction of the food makes with the sun. The distance is indicated both by the number of turns made in a given time, which decreases as the distance increases, and also by the number of waggles per turn which increases with the distance.

If the dance is carried out on a horizontal surface from which some blue sky is visible, the straight part of the dance indicates the direction of the food source. LINDAUER (1951, 1953) finds that exactly the same symbolism is used by dancers on a swarm to indicate the direction of a possible nesting site. However, the dances indicating sites last for much longer (up to an hour with intermissions) than those indicating food sources. This is intelligible from the point of view of biological function, since they are "calls" or instructions to a very large number of others. Their neurological basis may be greater intensity of drive.

The behaviour of Swiss and Dutch bees as described by TSCHUMI (1950), whose original paper we have not seen, and HEIN (1950), is more complicated. These bees appear to belong to the subspecies *A. m. mellifera*, but it is not, of course, known whether the difference in behaviour is always associated with the taxonomic differences between subspecies. According to HEIN, when the food source is at 2 metres from the hive the bee performs a "pull-dance" or "Rücktanz". It moves in an irregular path roughly towards the food on a horizontal surface or in the appropriate direction on a vertical surface, occasionally stopping to "point" in the direction while wagging its abdomen. At 8 metres it performs the "sickle dance", running back and forth in a semicircle whose axis runs in the appropriate direction, and wagging at each end of the path when facing in this direction. At 20 metres this is passing over into the figure of eight waggle dance described by von FRISCH, at 30 metres the transition is nearly complete, at 50 metres quite complete. RIBBANDS (1953 *b*) gives figures of these dances. However, even in this subspecies typical round dances are sometimes seen, and HEIN quotes TRIEBEL's observation that bees given dilute sugar water do not perform sickle dances.

Von FRISCH emphasises that there are considerable individual differences between bees in one hive. This suggests, but does not demonstrate, that these are segregating for genetic differences in "language". He emphasises that there are differences between hives; this similarly suggests differences in cultural traditions, since the individual bees in a hive are genetically diverse. If there were no cultural tradition tending to standardize the

behaviour of bees in a single hive, the differences between individual bees in a hive would, within a race, be about the same as those between averages characterising individual hives.

Bees troop behind the dancer keeping their antennae close to her body, before leaving for the place indicated.

Five questions may be asked, to all of which at least a partial answer can be given from von FRISCH's data.

1. How accurately is direction indicated?
2. How accurately are "instructions" as to direction followed?
3. Can we state in a simple manner the relation between the distance of the food (or more correctly the time or effort required to reach it), and the rhythm of the dance; as von FRISCH has stated the relation between the direction of the food and the direction of the dance?
4. How accurately is distance indicated?
5. How accurately are "instructions" as to distance followed?

The accuracy of communication of direction.

In any investigation of communication between animals, but more particularly where the message is quantitative, it is desirable to assess separately the accuracy with which a message is sent out, and that with which it is received.

In the case of the communication of direction by bees we have two ways of assessing the accuracy of the message sent out. We can compare the direction of the straight part of the dance, or of the bisector of the angle between two straight parts, with the direction expected on von FRISCH's theory. Secondly we can compare the *mean* direction taken by the bees with the true direction of the food. This comparison has the merit of being independent of any theory, and could have been made if no-one had ever observed the methods by which bees communicate. The individual bees which fly out in response to the message go in directions which have a fairly wide scatter round the correct direction. That is to say they have not, on the whole, responded very accurately to the message, unless indeed the dancer indicates different directions at different times, and is only accurate on an average.

There are two possible objections to the use of data recorded by a human observer. Since polarized light certainly alters the direction of the dance, it is possible that unpolarized or feebly polarized light affects it slightly. It is not impossible that light may affect the rhythm also. So the use of an observation hive may mislead in unexpected ways. Secondly, human observation may not be sufficiently accurate. We quote von FRISCH's words (translated by D. ILSE) regarding the "round dance". "At this distance [25 metres] for my own eyes the direction-giving waggling is not distinct enough to be perceived, but the bees seem to be much more susceptible to such hints."

A survey of the published work shows that human observations of

angles have a considerable bias. Thus in Table 4 von FRISCH (1948) records the following individual observations of dancing angles, when the solar angle, and therefore the theoretically correct dancing angle, was 66° : 53° , 60° (11 observations), 67° (3 observations), 68° , 70° , 75° (3 observations).

The probability that 15 or more out of 20 observed values should end in 0 or 5 is 1.4×10^{-7} unless the observer had a bias in favour of such numbers. So the bias is not in doubt. The mean is 63.85° , and its standard error calculated by the usual method is 1.4° , but there is undoubtedly a systematic error of unknown magnitude; though of course such observations are quite accurate enough to disclose the general principles of the bees' "language".

Very few observations have been published in which the accuracy with which direction is indicated can be deduced from the directions taken by the recipients of the message. In that recorded in Fig. 9 (1948) the scent plates were irregularly distributed. In those recorded on pp. 80 and 81 (1950), 7 plates were laid out at intervals of 15° along a quadrant of a circle of radius 200 metres with the hive as centre. The bees which gave the information had been fed on a plate 250 metres from the hive, in the direction of the central one of the 7 plates at which bees were counted. Numbering the cards $+3$, $+2$, $+1$, etc., beginning to the bees' right as they emerged from the hive, the numbers alighting on them were as in Table 1, according to von FRISCH (1950). Unfortunately, von FRISCH (1952) records the second of these experiments again. If this second account is correct, the right and left errors in the second experiment must be reversed. Had a complete circle of cards been provided, a few bees would probably have alighted on cards outside this quadrant, that is to say their error would have been over 45° . The fraction which flew to incorrect quadrants in two experiments (von FRISCH, 1948), in which cards were put out at 100 metres, was 4.8 %. It might have been less at a greater distance, and of course some of the stragglers may have been foragers which went out independently of messages from the returning bees.

In Table 2 we give the first four cumulants of these distributions, FISHER'S (1943) indices g_1 and g_2 of asymmetry and kurtosis, and the standard deviations. In such a case the calculation of k_4 is somewhat tedious, but it must be made if we are to give correct standard errors for the variance and standard deviation, which turn out to be over 30% higher than they would have been had the distribution been normal. The corrections for grouping have been made on the supposition that all bees crossing the 200 metres circle between $\pm 7.5^\circ$ from the correct point went to the central card, all those crossing it between $+7.5^\circ$ and $+22.5^\circ$ went to the first card to the right of it, and so on. The standard errors of g_1 and g_2 are those calculated for a normal distribution and thus measure the significance of deviations from normality.

Neither value of g_1 is significant, so there is no evidence that the distri-

butions were asymmetrical. On the other hand the value of g_2 is significantly positive in the first experiment, and on the verge of significance in the second. That is to say there were more extreme deviations than would be expected in a normal distribution with the variance actually found. A few bees outside the quadrant would have raised this value still further. On the other hand the removal from the counts of bees which had not received information from the dancers might have lowered it.

TABLE 1.
Data on errors of direction.

ERROR (in 15° units).	+ 3	+ 2	+ 1	0	— 1	— 2	— 3	TOTAL.
Experiment 1	8	13	58	132	37	7	3	258
Experiment 2	0	3	8	24	2	3	0	40

TABLE 2.
Analysis of data of Table 1.

	k_1	k_2	k_3	k_4	s
Experiment 1 . . .	+ .1860 ± .0606	.9481 ± .1182	+ .2133	+ 1.5828	.9737 ± .0607
Experiment 2 . . .	+ .1500 ± .1383	.7654 ± .2460	— .2437	+ 0.8517	.8749 ± .141
	g_1		g_2		
Experiment 1	+ .231 ± .152		+ 1.761 ± .363		
Experiment 2	— .364 ± .373		+ 1.454 ± .730		

The errors of the mean in degrees were $+ 2.79 \pm 0.91^\circ$ and $+ 2.25 \pm 2.07^\circ$. For the reason given above, the second error, which does not differ significantly from zero, should perhaps have a negative sign. On the other hand the standard deviations, round these slightly erroneous means, of the directions taken by individual bees, were $14.7^\circ \pm 0.9^\circ$ and $13.1^\circ \pm 2.1^\circ$. They do not differ significantly, and a weighted mean is $14.25^\circ \pm 0.84^\circ$.

The error in the mean direction of the bees flying out in response to a

dance may be taken as a measure of the inaccuracy with which the dancer in her dance taken as a whole, "described" the direction. The error is small, about 14 metres at a distance of 250 metres. In the more conclusive of the two experiments it was to the west of the correct direction, and can be entirely accounted for by the earth's rotation. The sun's apparent direction moves westward by about 1° in 4 minutes of time. If the direction communicated is the direction of the food source relative to the sun during the dancer's outward journey, and if 11 minutes, on an average, elapsed between this outward journey and the outward journeys of the

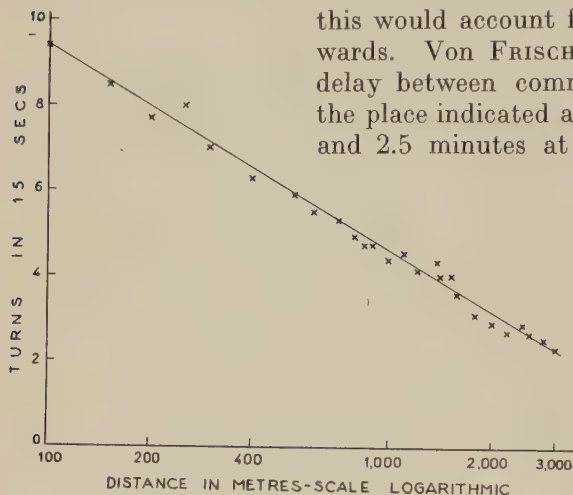


Fig. 1. — *Abscissa.* Logarithm of distance flown in metres.
— *Ordinate.* = Mean number of turns made in 15 seconds;
from von Frisch (1948). Line represents $n\ 4.76\ (3.95 - \log d)$.

bees which flew out in response to the dance, this would account for an error of 2.75° westwards. Von FRISCH (1948) gives the average delay between communication and arrival at the place indicated as 3.6 minutes at 400 metres and 2.5 minutes at 12 metres. The average time spent in gathering food and returning are not stated, nor is the average time spent in giving food to other bees before dancing. However, the total delay can certainly account for a large fraction of the error of the mean direction, and may account for all of it. The errors of individual bees round this mean were much greater.

They may largely be experimental artefacts. The distance between adjacent cards 15° apart on a circle of 200 metres' radius is 52 metres. A bee might very well fly between the central card and the adjacent one without perceiving either of them. If so, on finding nothing at 250 or 300 metres, she would begin to search more or less at random. Until the experiment has been repeated with cards at smaller intervals we cannot say that the standard deviation of 14° is a measure of the errors of individual bees in interpreting the dance. It is compounded of these errors and an at present unknown error due to the experimental conditions. We owe this important methodological criticism to conversation and correspondence with Dr. R. RIBBANDS.

Had the cards been very closely spaced there would certainly have been some dispersion round the mean. This could have been due to at least three causes.

(a) Some bees misinterpreted the dance, through sensory or motor inadequacy or faulty coordination.

(b) Some bees, having received information that the food was at

250 metres, did not stop in response to sensory stimuli from a card at 200 metres, but went on to 250 metres or more, and then began to circle in search of food.

(c) The form of the dance, whose straight parts diverge appreciably when food is found at distances less than about 600 metres, encourages a divergence of directions. If so, the angular spread would be less at greater distances.

The spread of the flight lines of individual bees round the mean direction, even if it is less than that calculated from von FRISCH's data, is perhaps greater than the optimum; that is to say causes the expenditure of more energy, on the average, for a given amount of food stored, than would a less spread. But a certain amount of spread must be advantageous for two reasons. The mean direction of the stream sent out must have a slight error due to "inaccurate" dancing, the rotation of the earth, and changes of wind. And in nature other flowers of the species indicated may be open near the flower "reported".

It is impossible to say what would be the optimal standard error for an individual, but it almost certainly exceeds the standard error of the direction of the mean. A similar problem arises in naval gunnery, where a superior force pursuing ships with less fire power should fire salvos with a considerable scatter, in the hope that at least one shell will hit a hostile ship and slow it down. A force with inferior fire power should concentrate its salvos, in the hope that several shells arriving simultaneously may sink a hostile ship, even if the probability of their doing so is not very high. Only a very detailed study would permit the calculation of the optimal value of the individual error for bees.

We may, however, assume that natural selection is always acting so as to reduce the error of the mean direction, while acting less intensely, if

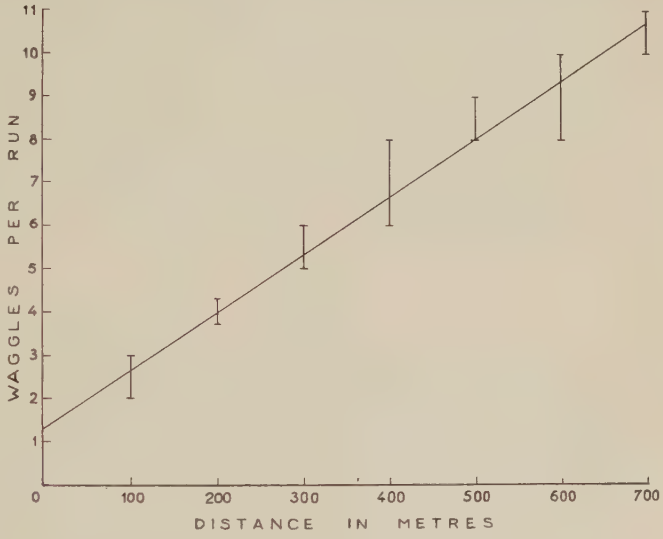


Fig. 2. — *Abscissa*. Distance flown in metres. — *Ordinate*. Number of waggles per straight run, limits given by von FRISCH (1946). Line represents $n = \frac{4}{3} \left(1 + \frac{d}{100} \right)$.

at all, to reduce individual errors which lead to a scatter round this direction.

LINDAUER (1952) has shown that the capacities both for dancing and for interpreting the dance are unlearned. However, they seem to improve with practice. Of 120 bees observed no less than 29 did not return from their first flight in response to a dance, several (including Nos. 19, 57, and 251) came back empty from their first such flight, but were later successful. 12 of the 91 successful bees returned with a load different from that indicated to them or from a different direction or distance. The indication of direction seems to be satisfactory from the first as judged by a human observer, but distance is at first overestimated. It is clear, then, that learning plays some part both in the dance and in the response to it.

By marking bees on the days on which they first fly out, it would be possible to discover whether the bees which made considerable errors in the direction of their flight were mostly inexperienced. It would be much harder, but not impossible, to determine whether the indication of direction improves with practice.

Ethological cybernetics.

WIENER (1948) defines cybernetics as "the study of messages and in particular of the effective messages of control". It has been applied to communication between men and between machines, but not yet to communication between animals. The communication of direction between bees furnishes a perfect example of a case where the amount of information transmitted can be measured. The theory of the measurement of information, as developed particularly by SHANNON and WEAVER (1949) is as follows. A unit of information is a choice between two equally probable alternatives, for example between a lamp being red or green, if it is known beforehand that it must be one or the other. If there are four equally probable alternatives, we have two units of information. If there are n equally probable alternatives we have $\log_2 n$, or $\frac{\log_{10} n}{\log_{10} 2}$ units of information, which is not usually a whole number.

In many cases there is a difficulty because the various alternatives are not equally probable, but this disappears in the case of the communication of direction. If a bee could only inform another that a food source was to the north or to the south of the hive, it could only convey one unit of information. If it could also signal that it was south and west, but no more, that is to say indicate the correct quadrant, it could convey two units. A choice from the series of 32 directions, North, North by East, North-North-East, North-east by North, and so on, used in navigation, conveys exactly five units. WIENER (1948, p. 76) showed that if, as the result of a "message", a quantity x which, in the absence of information,

could have any value over a unit range, say between 0 and 1, has a probability $f(x)$ of lying in a small interval between x and $x + \delta x$, the amount of information concerning it can reasonably be defined as

$$\int_{-\infty}^{\infty} f(x) \log_2 f(x) dx,$$

$$= \log_2 e \int_{-\infty}^{\infty} f(x) \log_e f(x) dx.$$

It follows that if the direction θ is at random in the absence of information as to direction (which is the case with round dances when the food source is within 10 metres), but after information is given θ is normally distributed with a standard deviation σ , then the amount of information which has been given concerning θ is

$$I = \log_2 \left(\frac{2\pi}{\sigma} \right) - \frac{\log_e 2\pi + 1}{\log_e 4}$$

$$= \frac{\log_{10} \left(\frac{360}{\sigma} \right)}{.301} - 2.0471,$$

if σ is expressed in degrees.

The correction when a distribution deviates slightly from normality is not large. It follows that if bees are spread out in directions with a standard deviation of 14.7° , each has, on an average, received 2.54 units of information. If we are right in believing that with a different arrangement of scent plates this standard error could be lessened, the correct amount may be three or four units. On the other hand the total "message" emitted by the dancer must be more precise. We have unfortunately only two data on the error of the mean of the stream of bees. In the two measured cases it was between 2° and 3° . That is to say it was more than $1/8$ and less than $1/4$ of the error of the representative bee. Thus it appears that the dance, as a whole, conveys about 5 units of information, and that each individual, on an average, receives over half, but not all, of this. This may not compare unfavourably with the performance of human beings when given complicated instructions.

It is not possible to make such accurate measurements of the amount of information concerning distance given by a dance, not only because, as we shall see, the data are fewer, but because all dances convey some information concerning distance, and we do not know what, if anything, a group of bees would do in response to a dance giving no such information.

It appears then that the dances to which the response was recorded each carried about as much information as does such a direction as "Sail North-West by West", but that the average amount of information received was somewhat less than is conveyed by such a direction as "Sail North-West", if it were known that this merely meant "Sail somewhere between NNW and WNW", and all courses taken lay between these directions.

This is perhaps an unduly low estimate, as the mathematical theory gives a good deal of weight to the few stragglers, and some of them may not have received any information at all.

This analogy enables us to compare the accuracy of bees' direction indication with that of man, without any mathematics. A direction to one point of the compass, e.g. "West", has a maximum error of 45° , and an average of $22\frac{1}{2}^\circ$. Similarly such a direction as "NW by W" has an average error of one eighth of this value, or 2.8° , which is just the error found for bees' dances.

We shall see later that the indication of distance is about as accurate as the indication of direction, perhaps slightly less. Dances also give some information as to the number of workers needed, but this is much less precise. However, we shall perhaps not be very far out if we suggest that a dance gives about 5 units of information as to direction, 4 to 5 as regards distance, and 2 to 3 as regards number of workers needed, the total being about 12 units, besides the information given non-symbolically by the odour. A human language in which about 4,000 phrases, but no more, were possible, along with demonstrations of objects found, would give the same amount of information, if combined with demonstrations of objects. Such a language would require much less than 100 words, and a code of all possible combinations of 3 letters would more than cover it. A human language differs from bee communication in that the different phrases are sharply separable, whereas bee dances grade into one another. But each is susceptible of quantitative analysis. Judged in this way the vocal repertory of birds seems to be considerably smaller, even when they have learned a number of human phrases.

The indication of distance.

The character of the dance depends mainly on the distance of the food source. But the rhythm is slowed down, not only by an increased distance, but by an adverse wind on the bees' outward journey; similarly it is speeded up by a wind which aids the bee on its outward journey. When a detour in a journey is necessary, the dancing bee indicates the direction without reference to the detour, but includes the detour in its information as to the distance. Thus it would be more accurate to state that the dance gives information as to the energy spent on the outward journey, which is only correlated, though it is highly correlated, with the distance.

As the corrected distance increases the dance changes in the following ways. 1. The number of turns executed in a given time diminishes. 2. The number of abdominal movements executed during each straight part of the dance increases. 3. The spatial length of the two parts of the dance in which the bee takes a straight path increases. 4. The angle between these two straight runs diminishes to zero (Table 3, 1948).

3 and 4 are not very consistent. Thus von FRISCH (1946) writes "At 100-200 m. it [the straight run] extends roughly 1-2 cell diameters, at 400 about 2 or 3, and at 1,000 about 3-4, but these distances are not strictly adhered to." And though the divergence between successive straight runs falls off with distance "There are, however, great differences to be observed among individual bees" (von FRISCH, 1948).

The most complete data exist on 1: the number of turns made in a given time. Von FRISCH (1946) gave numerical data on two different hives; (1948) a graph which averaged data from a number of hives for distances from 100 to 3,000 metres; (1950) a graph for averaged data from a number of hives for distances from 100 to 6,000 metres; and (1952) a graph giving a few data on distances up to 11 kilometres. The last two graphs are on too small a scale to permit very accurate reading. It is also clear that all the data for distances over 3,000 metres are based on 773 or fewer observations. They are very irregular, and do not fit the curve drawn by him at all closely.

The data up to 3,000 metres obey a very simple law. The numbers of turns made in a given time is proportional to a constant minus the logarithm of the distance flown. In Table 3 the average numbers of turns made

TABLE 3.

Numbers of turns in 15 seconds as a function of distance.

d (metres).	n_1 (hive K).	n_2 (average).	n (calculated).	$n_1 - n$	$n_2 - n$
100	9.5	9.4	9.4	+ .1	0
150	8.5	8.5	8.4	+ .1	+ .1
200	7.7	7.7	7.8	— .1	— .1
250	8.1	8.0	7.4	+ .7	+ .6
300	7.1	7.0	7.0	+ .1	0
400	6.6	6.3	6.4	+ .2	— .1
500	6.1	5.9	6.0	+ .1	— .1
600	5.9	5.5	5.6	+ .3	— .1
700	5.0	5.3	5.3	— .3	0
800	—	4.9	5.0	—	— .1
850	4.8	4.7	4.9	— .1	— .2
900	4.7	4.7	4.7	0	0
1,000	4.5	4.4	4.5	0	— .1
1,100	4.5	4.5	4.3	+ .2	+ .2
1,200	4.2	4.1	4.1	+ .1	0
1,300	4.3	4.3	4.0	+ .3	+ .3
1,400	4.1	4.0	3.8	+ .3	+ .2
1,500	4.0	4.0	3.7	+ .3	+ .3
1,600	—	3.6	3.6	—	0
1,800	—	3.1	3.3	—	— .2
2,000	—	2.9	3.1	—	— .2
2,200	—	2.7	2.9	—	— .2
2,400	—	2.8	2.7	—	+ .1
2,600	—	2.7	2.5	—	+ .2
2,800	—	2.5	2.4	—	+ .1
3,000	—	2.3	2.3	—	0

in 15 seconds after flying for various distances are tabulated. n_1 is taken from von FRISCH's (1946) Tables 4 and 5, and refers to hive K. Where a choice is open, his Table 5, which is based on more data, is preferred. n_2 is read off from his (1948) Fig. 1, based on averages from a number of hives. n is calculated from the formula

$$n = 4.76 (3.95 - \log_{10} d) \dots \dots \dots (1)$$

where d is the distance in metres. $n_1 - n$ and $n_2 - n$ are the differences between observed and calculated values. It will be seen that only one value of $n_2 - n$ exceeds 0.3. Von FRISCH noticed the divergence of this value from his graph, and wrote "observations for this distance were nearly all taken from a single colony [presumably hive K] with an unusually quick dance". The difference $n_2 - n$ is usually less than the standard error (or perhaps probable error) shown in von FRISCH's graph, and much less than half the range. The values of $n_1 - n$ are mostly positive, and a slightly different formula could easily have been found which fitted the results better. But it is probably not worth using refined methods for fitting unless the data are given in full, so that the appropriate weight can be assigned to each observation. Our Fig. 1 shows von FRISCH's value n_2 as a function of $\log_{10} d$, with the line corresponding to formula (1).

Formula (1) is clearly a good guide to prediction over the range from 100 to 3,000 metres. But it does not fit the data for greater distances given in von FRISCH's Fig. 3 (1950) and Fig. 14 (1952). The former extends to a distance of 6,000 metres, the latter to 11,000. Formula (1) consistently predicts a number of turns smaller than that observed. The graphs are on too small a scale to read very accurately, but at 6,000 metres about 1.7 turns were observed, and 0.8 calculated, at 10,000 about 1.2 were observed, and 0 calculated. The data between 3,000 and 6,000 metres are rather irregular, and doubtless based on rather few counts. Some bias may perhaps have been introduced if a bee which made no turns during 15 seconds was not counted as dancing. However, there can be little doubt that beyond 3,000 metres the rhythm falls off more slowly than is predicted. We shall later suggest a theoretical basis for the validity of formula (1) over a certain range, and show that an analogous formula applicable to human performances breaks down in a similar way. If it were universally valid a bee would be unable to signal distances exceeding 9 kilometres.

Formula (1) may be written as

$$\text{or} \quad n = 4.76 \log_{10} \left(\frac{8,910}{d} \right),$$

$$\text{or} \quad n' = \log_2 \left(\frac{8,910}{d} \right),$$

$$d = 8,910 \cdot 2^{-n'},$$

where n' is the mean number of turns made in 10.47 seconds. Thus the two constants in the formula define a standard distance of about 9 kilo-

metres at which the frequency of turning would fall to zero, and a standard time of about 10.5 seconds, such that a doubling of the distance subtracts 1 from the number of turns made in this time, or an addition of 1 to the number of turns halves the distance indicated.

The number of waggles, or “double tail movements” performed during each straight run is, on the other hand, roughly a linear function of the distance indicated, up to 700 metres. Table 4 gives the numbers observed by von FRISCH (1946) and those calculated from the formula

$$n = \frac{4}{3} \left(1 + \frac{d}{100} \right), \quad \text{or} \quad d = 75 n - 100. \tag{2}$$

It will be seen from Table 4 and Fig. 2 that this formula fits the data reasonably well, within the rather wide ranges given. It will be of the greatest interest to discover whether this simple relation continues to hold good at higher distances. As von FRISCH pointed out, these movements cannot be counted reliably by a man without mechanical aid, and anyone who has tried to do so cannot but be impressed by von FRISCH's results. It is to be hoped that they will be recorded by cinematography, which could be done with red light without disturbing the bees if a strong white light did so.

It may be remarked that the number of waggles performed in 15 seconds increases from about 30 after a flight of 100 metres to about 55 after a flight of 600 metres, and must then decrease again if the above formula

TABLE 4.

Numbers of waggles per straight run as a function of distance.

<i>d</i> (metres).	<i>n</i> (observed).	<i>n</i> (calculated).
100	2-3	2.7
200	about 4	4.0
300	5-6	5.3
400	6-8	6.7
500	8-9	8.0
600	8-10	9.3
700	10-11	10.7

holds good for higher distances. Only the number of waggles per straight run appears to bear any simple relation to the distance of the food source.

In 1946 von FRISCH wrote: “I do not know whether the slowing up of the turns or the increase in the number of waggle movements is the more important from the point of view of perception by the bees.” In 1950 he wrote: “The bees in the hive can only understand the meaning of the dancer's rate of turning and can perceive the distance they must fly to

reach the food." Because the rate of turning is much easier for a human observer to count than the rate of wagging, it does not follow either that it is more accurately perceived by bees, or that it has more influence on the behaviour of bees which perceive it. "For often", to quote von FRISCH again, "nature reaches her goal by another path, where man cannot see his way." RIBBANDS (1953 *b*, p. 140) agrees that the number of waggles per run may be more important than the tempo of the dance.

If it is found that formula (2) holds at greater distances than 700 metres, it will perhaps become more probable that it is the basis on which at least the longer distances are communicated. It is difficult to see how formula (1) or any analogous formula could give sufficiently accurate information as to distances over 1 kilometre. The range in the number of straight runs observed in 15 seconds was always at least 1, except for hive K at 1,500 metres. This corresponds to an error of + 62% or—38% in the distance indicated, which would be very serious at a distance of several kilometres. If we suppose that each potential new forager follows the dancer for as long as a minute, which we think is a considerable overestimate, the error would still be + 13% or—11.5%. On the other hand, an error of 1 in the number of waggles observed per run would produce an error of only 75 metres in the distance indicated. As the potential gatherers usually follow a dancer during several turns of dances corresponding to short distances, this error would be reduced.

We think, then, that there is a strong *prima facie* case for the hypothesis that, at least for long distances, the number of waggles per run, rather than the number of turns per minute, is the main indication of distance. The question should ultimately be decided not only by further observations to test the validity of formula (2) or a more accurate but similar formula, but by experiments in which scented model bees or dead bees were mechanically moved in "dances" in which the frequency of turns and that of waggles was varied independently.

If the simple formulae (1) and (2) are found to hold good in general, over the ranges of distances given, it will be possible to describe each of the two methods of distance communication in terms of two parameters. Von FRISCH's evidence suggests that for hive K the parameter 3.95 should be replaced by 3.97, the parameter 4.76 being unchanged. It should be possible to determine these parameters, as "linguistic" characters for different hives, and to see, for example, whether, like the form of the dance, they vary between different races.

The accuracy of distance communication.

Unfortunately only one experiment has yet been published which gives data on this question, and it was not so designed as to facilitate statistical analysis (von FRISCH, 1952, p. 282). The results are summarized in Table 5. The food source indicated by the communicating bee was at

750 metres. Scent plates were put out in the correct direction at the distances from the hive shown in the first row of the table. In the second row their distances from the indicated goal are shown. The third row is calculated as follows. The bees which alighted on the card 1,000 metres away from the hive may be supposed to have sought for food anywhere between 900 and 1,250 metres, these being the mid-points between the plate at 1,000 metres and its neighbours. The mid-point of this stretch was at 1,075 metres, or 325 metres beyond the goal. There is no way of grading the farthest card, and we have arbitrarily made no correction.

The second row of Table 5 gives an error of + 31.8 metres, or 4.2 % of the correct distance, for the mean. The third row gives an error of + 45.1 metres, or 6.0 %. If the six extreme results were omitted, we should have errors of + 32.2 and + 38.0 metres. The standard deviations cannot be calculated exactly as the grouping was irregular, but are some-

TABLE 5.
Errors in distance.

Distance from hive ..	75	200	400	700	800	1,000	1,500	2,000	2,500
— goal ..	— 675	— 550	— 350	— 50	+ 50	+ 250	+ 750	+ 1,250	+ 1,750
(adjusted)	— 662.5	— 531.25	— 325	— 100	+ 75	+ 325	+ 750	+ 1,250	+ 1,750
Number of bees.....	4	0	10	17	30	12	2	0	2

what under 390 metres in each case. However both the distributions are very leptokurtic, owing to the 4 bees which stopped at 75 metres, and the 2 which went on to 2,500 metres. If these were omitted, we should have standard deviations of about 210 and 230 metres, which probably convey a better idea of the actual variation round the mean. Even if we take these low values, the deviations of the mean from 750 metres are not significant. We cannot say that if more bees had been counted, the mean might not have fallen short of 750 metres.

If at a distance of 750 metres, the spread of angular deviations round the mean would have been the same as at 200 metres, the standard deviation in a lateral direction would have been about 180 metres. We saw reason to suspect that it might have been less.

To sum up, this one experiment suggests that the dance as a whole conveys information concerning the distance whose error may be of the order of 5 %, or considerably less, but that the deviation of individual bees in range, that is to say along the line of flight, is somewhat greater than their lateral deviation, but not more than twice as great. A few more observations, especially if the two kinds of error were measured simultaneously, would however give a much more definite answer to this question.

The duration of dances.

Von FRISCH (1923, p. 33) gives data on the duration, in seconds, of the round dances performed by 101 workers which had returned after collecting sugar water near the hive. 68 only danced in one place, the others in up to six different places.

First consider the total times spent by each bee in dancing. The range was from 1 second to 125 seconds, the mean being 24.27 seconds, the standard deviation 26.1 seconds. The distribution is highly skew positively, with $g_1 = 5.84$. The longer periods of dancing were usually broken up so that a bee whose total dancing time was long usually danced in several places. Table 6 shows that the mean length of time spent in

TABLE 6.

NUMBER OF PLACES where dances occurred.	NUMBER of bees dancing.	MEAN TOTAL dancing time.	MEAN DANCING time per place.
1	68	13.89	13.89
2	21	30.71	15.36
3	6	53.67	17.89
4	3	69.00	23.00
5	1	109.00	21.80
6	2	112.50	18.75

dancing in each place did not increase greatly with the number of dances. None of the differences between numbers in the last column are significant.

The striking fact is the extreme variability in the length of the total dance, the coefficient of variation being 107.7 %. All these dances were performed after drinking sugar water near the hive. It is not clear from the context whether the amount of fluid and the sugar concentration were constant, but this seems probable. If so, the duration of a dance is far less standardized than its other characteristics.

It is certain that the threshold at which sugar in the water given to bees excites dancing varies with the needs of the hive. LINDAUER (1949) and RIBBANDS (1953 *b*) have shown that it is under many other influences. If dancing occurs at all, it is clear that its duration varies greatly between individuals. This is intelligible, for a bee cannot estimate the amount of food available for others with great accuracy, and the harm done by calling too few bees, at least, is negligible compared with that which would be done by communicating direction or distance incorrectly.

Bee « language » and human logic.

We began these calculations to explore the resemblance between bee dances and human methods of communication which von FRISCH emphasises by his use of the word "Sprache".

In the terminology of PEANO and RUSSELL each dance is a propositional function with four variables; and its simplest translation into human words is perhaps "There is a source of food smelling of A, requiring an effort B to reach it, in direction C, of economic value D". The items B, C, and D are quantitative. A human being would give them in words, such as "400 metres WNW, requiring 9 workers". The bees' symbolism is like that of an analogical calculator such as a slide rule or a speedometer, which represents one continuously variable magnitude by another. The human symbolism is like that of a digital computer such as an ordinary calculating machine or a mileometer, which represents it by one of a discrete series of symbols.

From the standpoint of formal logic such verbal communications are almost always false. A distance is not exactly 400 metres. A formally correct statement might be "between 350 and 450 metres". The form of human communication which most resembles the bee dances is the clock, which is also similar in using the vertical to symbolize a direction of the sun. The recording of time in words introduces an error which is vivid to ethologists. If actions *a*, *b*, and *c*, are recorded as happening at 10.44, 10.46, and 10.47, we may have thrown away the information that 175 seconds elapsed between *a* and *b*, but only 6 seconds between *b* and *c*. A further subdivision of the time units would not alter the impossibility of precision which is inherent in an Aristotelian logic obsessed by the attempt to describe what is indefinitely complex in a finite number of words with fixed meanings. The many-valued logic of TARSKI and LUKASIEWICZ is an effort to overcome difficulties which do not arise in the communicatory method evolved by hive bees. But just because bee communication is so well suited for conveying quantitative information, it is probably less flexible than human language. RIBBANDS (1953, *a*) showed that bees do not communicate the colour of a food source.

Our consideration of bee "language" has inevitably raised a problem which human logicians have hardly considered. A highly complicated statement is said to be true or false, and to convey so much information, if a sufficiently educated and intelligent hearer could extract certain information from it. The statements "If, and only if, *Mustela putorius* is a member of the Entomostraca, Rangoon is the capital of Siam" and "Rangoon is not the capital of Siam" are "logically equivalent", but the latter conveys more information to most people. Our analysis of bee communication has compelled us to ask, and permitted us partially to answer, the two questions "How much information could a given communication convey to a well-equipped and attentive recipient?" and "How much did it convey to the average recipient?" Human logicians might well ask the latter question more frequently.

The use of quantitative rather than "verbal" communication is not confined to bees. LORENZ (1949) has pointed out that the number of syllables in a "phrase" produced by *Anser anser* is about ten when at rest, diminishes when moving forward on the ground, and is reduced to

one during flight. This may be compared with the slowing down of the bees' dance rhythm as the journey is lengthened.

Evidence that the dance is a prediction rather than a description.

The function of the dance is to induce other bees to fly for a prescribed distance in a prescribed direction, either in search of food or water, or as members of a swarm. We are not however justified in assuming that a dancer has this purpose in mind any more than a human being looks forward to the oxygenation of his blood when breathing, or to persuading others to go to bed when yawning involuntarily. We can ask with what other activities of the bee's central nervous system the dance is most closely correlated. It could perhaps be legitimately described as one of: 1. An account of the last outward flight. 2. An account of the last homeward flight. 3. A prediction of the next outward flight. 4. An account of the location of the food source.

We can eliminate 1 because a scout may only have discovered a food source after prolonged wanderings, but the dance indicates a direct flight if this is possible. We can eliminate 2 because the rhythm is slowed down, indicating a greater effort, if the wind helped the bee back to the hive, or if the return flight was down hill (HERAN & WANKE, 1952) and conversely. 4 is a highly abstract idea. Most human beings think and speak in terms of journeys rather than distances. When the dance is performed on a level surface, the straight run is made in the correct direction; moreover the direction relative to the sun is that at the moment of dancing, or a few minutes earlier. If there were a fixed scheme, corresponding to a map, in the bee's brain, it would still have to alter the dance expressing it throughout the day. How the bee "knows" in which direction it must fly we shall not discuss here. Its behaviour leaves no doubt that some sort of a scheme for the next flight exists in it.

A British worker, in correspondence, has contested the view that the dance is a prediction on the ground that he has never observed a dance by a returning forager after her first visit to a new source. LINDAUER (1948) found that bees often did not begin dancing until they had visited a food source five or more times. This was an invariable rule when the sugar solution provided was so weak as only just to promote dancing at all. However when the sugar concentration was raised to four times this threshold value, LINDAUER found that about half the bees danced on their first return, and when it was raised to eight times the threshold, almost all of them did so. Clearly the repeated finding of food at one spot increases both the frequency and duration of dances, as does a high concentration of sugar or the addition to it of certain scents.

Further the dance (when indicating a food source, but not a nesting site) is immediately followed by an outward flight. LINDAUER (1951) writes of the dances indicating site directions, "During this time the bees

concerned did not dance continuously, but they also did not fly away, as food-gathering bees do in all haste, when they have finished dancing".

Another argument leads to the conclusion that a dance is to be regarded as a preparation for a flight. VON FRISCH (1923) notes that when a bee is given a little sugar water, it does not extrude its scent organ, nor does it dance. If the amount of sugar is increased, it still does not at once extrude its scent organ, but dances on its return to the hive. At the end of its next outward flight it flies round the food source for a time up to a minute, extruding its scent organ. It then feeds, extruding its scent organ from time to time, thus attracting other bees, which may have participated in its dance, to the exact spot where food is present. RIBBANDS (1953 *b*), however, states that the correlation between dancing and subsequent scenting is not absolute. Thus the dance usually predicts, but does not report, the extrusion of the scent organ, which is certainly a simpler, probably a phylogenetically older, method of communication than the dance. It may have originated as a signal for the recognition of females by males (JACOBS, 1924). Such a displacement of a sexual signal is not unparalleled. Male guineapigs (*Cavia porcellus*) make a very characteristic bubbling grunt when courting females. One of us has occasionally heard females make this sound, though not for long at a time, on finding very succulent food.

A further argument can be deduced from the way in which the rhythm falls off with distance. The linear relation between the frequency of turning and the logarithm of the distance at once suggests WEBER and FECHNER'S law. However, another interpretation is as follows. HILL (1927) found that if he plotted the mean speeds of human beings when making athletic records (skating, running, and walking) against the logarithms of the times taken, he obtained nearly linear graphs over a fairly wide range, apart from short distances such as runs of less than 200 metres, where an appreciable fraction of the time was spent in acceleration. Cycling and swimming records yield similar graphs, and the results are similar if the logarithm of the distance is substituted for that of the time.

We suggest that a bee, like a human athlete, may move more slowly even at the beginning of a long journey than at the beginning of a short one, and that the number of turns executed per minute may be proportional to the speed at which it is going to fly. There is probably a speed involving a minimum energy expenditure per metre, higher or lower speeds being less economical. On a short journey the bee could afford to waste some energy by flying a good deal faster than this speed; on a longer journey it would have to be more "careful". The onset of fatigue in insect muscles may follow the same laws as that in mammalian muscles. If so, the speeds of bees' journeys may be expected to fall off with the logarithm of the distance as in man.

Both for bees and men the linear relationship ceases to hold beyond a certain distance (except for human skating records). Thus the mean

speed in human running records falls off less rapidly between 5 and 25 kilometres than would be expected from the speeds between 400 metres and 5 kilometres. In the same way the numbers of turns made by a dancing bee in 15 seconds falls off more slowly at distances beyond 3 kilometres than would be expected from formula (1).

This hypothesis will be disproved or supported by measuring the times taken to fly various distances. PARK (1923, 1928) found that the speed of bees returning to a hive after correction for wind was fairly constant (13-16 m.p.h.) while that of out-going bees was much more variable (7-18 m.p.h.) with a slightly lower average. Nothing seems to be known of speed as a function of distance or information.

The hypothesis is supported by the fact that bees adjust their food supply to the journey which they intend to make. BEUTLER (1950) found that the alimentary canal of bees setting out to collect syrup or water near the hive contained about 1 mgm. of sugar; those about to gather syrup at 500 metres contained 1-1.5 mgm.; those intending to gather syrup at over 1 km. contained nearly 3 mgm.; while pollen gatherers contained nearly 4 mgm. If a bee adjusts its food supply to its future task, it may well adjust its flight speed.

These facts, then, are all compatible with the view, which we develop later, that the dance is a highly ritualised *intention movement* (1). If so it is not unique. The characteristic pose of a pointer dog is clearly an intention movement arrested in such a way as to give fairly accurate information as to the direction of game to human sportsmen. Occasionally the dog does not arrest the movement, and its intention quality becomes very obvious. Setters show a similar behaviour pattern. BURNS (1952) gives a valuable discussion of the behaviour of collies known as "showing eye", which appears to be an arrested intention movement, and of its genetical determination.

The comparison of the bees' dance with such "derived activities" should perhaps be credited to ARISTOTLE, if TINBERGEN'S (1952) interpretation of the post-copulatory movements of hens as displacement activities is accepted.

The evolution of bee communication.

The more biologically important activities of animals (including men), for example feeding, excretion, copulation, catching prey, fighting, and escape, are often preceded by others usually involving less expenditure of energy, and of less obvious utility to the species. These include inten-

(1) The term "intention movement" is perhaps unfortunate, since "intention" refers to a subjective phenomenon in men. In discussing an example of such a movement DARWIN (1878) wrote of pointing in dogs: "The act of pointing is probably, as many have thought, only the exaggerated pause of an animal preparing to spring on its prey." Such an expression as "preparatory movement" might cover such cases, and also, for example, rudimentary nest building activities many months before a nest is actually built.

tion movements. They include what are believed to be specializations for communication (ritualizations) "derived" (HUXLEY, 1923, TINBERGEN, 1952) from intention movements, displacement activities and similar activities. They also include conditioned reflexes of the second kind (KONORSKI, 1950). We suspect that intention movements, like many displacement activities, are always a symptom of conflict of drives. The drive whose incomplete expression is the intention movement is competing with another drive. If an intention movement is seen to incorporate features appropriate to the satisfaction of yet a third drive, it is classed as a displacement activity.

We shall use the word "prelude" to describe these three classes of movements, and any others which have this temporal relation to a succeeding activity which is usually of greater biological importance to the organism which makes it. This word is intended to be independent of any hypothesis as to the causal relations of such movements, that is to say their physiological mechanism, their function in the animal's life history, their development in an individual ontogeny, or their evolutionary history. These are matters of interpretation which may change; we are trying to use a terminology as objective as possible. While we think that bees' dances may best be regarded as intention movements, we wish to discuss them in terms which will remain valid if that interpretation is not accepted. Etymologically a prelude means a game, that is to say an unimportant activity, performed beforehand. *Ludus*, incidentally, denoted intellectual exercises performed at school, as well as play.

Any prelude can be regarded as a means of communication, even if it does no more than reveal an animal's probable future activity to an ethologist. But it often acts as a signal to other animals; and both the nature of the movement and the reactions of other animals to it may suggest strongly that it has been modified in the course of evolution to take on a communicatory function (TINBERGEN, 1952).

Signals between animals, including releasers (1), are classified according to the receptors by which the recipient receives them, and not usually by the effector organ of the communicator. Thus raising of a crest of feathers and expansion of chromatophores are both described as visual signals. Tail movements of reptiles in threat are classed as visual unless, as in *Crotalus*, they cause an obvious sound. Most signals are chemical (olfactory), visual, or auditory. We have suggested that a bee following a dancer on a vertical surface is led to fly in a given direction by a combination of kinaesthetic stimuli due to its own movements and stimuli from

(1) We use this word to mean "Any specific feature or complex of features in a situation eliciting an instinctive activity, or mood" (THORPE 1951). We must not be assumed to agree with LORENZ, (1935, 1937) definition, still accepted by TINBERGEN (1953). "The means evolved for the sending out of key stimuli..." Such a definition on the face of it assumes a teleological view which we do not share. What is perhaps even worse, it implies that we cannot describe a structure or function as a releaser unless its evolutionary history is known, which is never the case. In fact an instinctive action, such as the opening of a nestling's mouth, may often have served other purposes before it became a releaser.

baroreceptors (probably JOHNSTON'S organs), which are best regarded as proprioceptors. According to von FRISCH'S theory the distance flown is regulated by the number of turns made in a given time. If so, the communication is kinaesthetic. If our view is correct that the number of abdominal waggles per straight run is an important distance signal, then part of the communication may be through antennal receptors. When the dance is followed on a horizontal surface illuminated by the sun or by polarized light, there is of course a visual component in the signal. But it appears that the main components are kinaesthetic, and auditory in the extended usage of PUMPHREY (1950), or perhaps tactile.

Some preludes, considered as signals, evoke an activity in the recipient Y which is different from the activity in the communicator X to which they are a prelude. Examples can readily be found in courting signals. Others evoke a similar activity in Y, for example alarm calls in some birds. In this latter case it is often biologically advantageous if Y can perform the prelude as well as the principal action. For example an alarm call can be broadcast through a flock of birds. Deliberate imitation is rare in animals (SPALDING, 1873, THORPE, 1950, TINBERGEN, 1951). However, the imitation of sound is common in birds. McDUGALL (1928) points out that this is so because the sound made by Y produces similar changes in its nervous system to a like sound made by X, which is not the case for many other activities, and because connexions have been established between Y's auditory and vocal motor systems. To be efficient, Y must have the capacity to imitate the cry, which may or may not involve a learning process, *and* the behaviour pattern of repeating it immediately it is heard. When both exist together, unanimous action of a flock may result. This provides a selective advantage explaining the evolution of this capacity which puzzled LORENZ (1952, p. 89). The mimicry of men volunteered by parrots and corvines shows a remarkable insight when it is hypothesised that they are interpreting our speech as preludes which we make to secure unanimity of group action. Our colleague Miss J. M. CLARKE has had a parrot for eighteen years who prefaces throwing his seed about by saying "Want some grain". A parrot cannot be taught to ask for food under the internal stimulus of its own hunger. It can teach itself the language of its gaolers to offer them food, or to entice them to eat with it.

The other case where a prelude is readily imitated is where it is a form of locomotion, or "dance", and Y performs the prelude if it follows X, lured by some stimulus such as a smell emanating from X. We suggest that this applies to bee dances, and probably to some of the "ritual dances" of birds discussed by ARMSTRONG (1947). Whether repeating a cry and following a dance are "true" imitations (ARMSTRONG, 1951; HINDE, 1953, *a*) could only be decided by reference to an animal's consciousness.

We further suggest that in many cases a prelude, *for whatever reason it is performed*, induces the mood appropriate to the subsequent action. This is clearly so for some human actions. Shakespeare's King Henry V

(Act 3 Scene 1) commands his soldiers to carry out prelude movements of the facial and other muscles before an attack. By inhibiting preludes to flight, such as trembling and screaming (which is particularly difficult if others are trembling and screaming) a human being can inhibit himself from yielding to the escape drive, and so on. This is simply a restatement, in more objective terms, of the theory of emotion due to LANGE and JAMES (1891).

It is probable that a bird, by repeating the alarm note first uttered by another, not merely informs other members of the flock, but brings itself into the mood for escape. This would be hard to prove. It is much more plausible that a bee, by following, and therefore automatically imitating, the dance of another bee, brings itself into the mood to fly out in search of food.

On this hypothesis we can give an account of the evolution of communication in bees. We have to explain how a two-way neurological connexion between dancing and flight was established, that is to say how on the one hand a given intended flight came to be preceded by a dance corresponding to it with some precision, and on the other hand participation in the dance came to cause the participants to fly for an appropriate distance in an appropriate direction.

We suggest that the round dance, which does not indicate direction or distance, is the phylogenetically oldest form of the dance. If a species were observed at this stage of evolution, we should perhaps say that the dance indicated a drive in the dancer to seek food, and that participation in it released food-seeking activity in others. Ethologists would describe it as a social releaser. There might be some controversy as to whether it was to be regarded as "derived" from an intention movement, or as a displacement activity due to the conflict between the drives to seek food and to remain in the hive. A small bee community of a thousand or less individuals could often find all its food within a hundred metres, and the round dance sufficed for its needs. The participants searched at random for flowers whose smell was carried by the dancer. The gradual evolution of the instincts for dancing and for response to the dance led to the establishment or enhancement of neurological connexions between the centres concerned in flying and walking.

The evolution of the round dance made food gathering more efficient, increased the size of the community, and therefore made directive communication advantageous, if it was possible. Straight runs in a given direction on a horizontal surface indicated intention to fly over 100 metres in a given direction; and once the flying and walking centres were coordinated, their imitation tended to steer participants in the same direction. This was valuable long before the coordination had become as precise as it is in modern hive bees. If we are right in suggesting that the rhythm of the dance is correlated with the speed of the intended flight, the indication of distance by rhythm developed along similar lines.

The work of BIRUKOV (1953) and VOWLES (1953) (the latter only avail-

able to us at the time of writing in RIBBANDS' [1953, *b*] summary) suggests how a dance on a horizontal plane was "translated" into one on a vertical plane. BIRUKOV studied dung beetles, *Geotrupes sylvaticus*, which were walking in approximately straight lines on a rough horizontal surface under photomenotactic orientation by a light source. On substituting a diffuse light, and making the surface vertical, he claims that the beetles then move so that the nadir (not the zenith as in bees) corresponds to the former light source. His results so far published do not support this claim completely. In each of the ten experiments shown in his Fig. 1 and 2 the beetle, under the changed stimuli, either continued in its former path or turned through approximately 180°. Nevertheless, some sort of equivalence between photomenotaxis and geomenotaxis is clear. VOWLES apparently found that in ants (species not stated by RIBBANDS) the zenith corresponds to the light direction, as in bees. The receptor organ for gravity appears not to be a statocyst, as BIRUKOV suggested, but JOHNSTON'S antennal organ. The physiology of these reactions will presumably be cleared up by experiments like those of von HOLST (1950) on fish, on the interaction of the two stimuli, rather than the mere substitution of one for the other. But it is clear that, given any sort of directional dancing on a horizontal surface, the species ancestral to hive bees would have danced on vertical surfaces so as to give some kind of indication, perhaps not very accurate, but capable of improvement by natural selection.

We can thus give a hypothetical account of the gradual perfection of the communicatory system which is the basis of von FRISCH'S current theory. If, however, we are correct in suggesting that the number of waggles per straight run is an important indicator, and perhaps the principal indicator, of distance, the evolution of this process cannot readily be explained as above, since the bees which follow a dancer, if they oscillate their abdomens at all, do so with much less amplitude than the dancer. Rhythm may well be an adequate indicator of distance for distances up to 1 kilometre or so. If so, indication by waggle number is probably a late development, which only became useful when very large populations made occasional long flights advantageous. We can again regard the waggles as ritualized movements, each waggle indicating the "intention" to fly another 75 metres, but it is not clear how the waggle originated, or how it activates the bees which follow the dancer.

However this subsidiary question is answered, the dance is, we think, according to the usual definition a social releaser, and the response to it involves an innate releasing mechanism. If this interpretation is not accepted, the neutral word "prelude" may be used. The above account of the evolution of the dance is, of course, hypothetical, and is unlikely to be correct in all respects. It has the merit that the communicatory system would be of some use at each stage, and that each further step would be selectively advantageous. Once an equivalence between flight and walking had been established, this could be further evolved, and the same developmental change which made for greater accuracy in the direc-

tion and rhythm of the dance before a given flight would also make for greater accuracy in the direction and distance of flight after a given dance. The prelude and the mechanism of response to it are thus part of the same process, and naturally evolve in parallel. Physiologists take this sort of equivalence for granted in the case of processes which are simultaneous or almost simultaneous, for example the contraction of a limb muscle, the relaxation of its antagonists, and the proprioceptions which accompany them. It is more surprising in the case of processes more widely separated in time, but may be commoner than is thought; for example such an equivalence may exist between contractions of vertebrate eye muscles and subsequent contractions of the limb and body muscles.

When more data are available it will also be necessary to consider the evolution of the dance as a means for directing a swarm. In this context the dances last much longer, which is biologically advantageous, since the more bees can visit the chosen site and later act as guides for the swarm, the better. The dances executed on the swarm do not seem to differ from food-indicating dances in other respects. It is possible that the nest-site indicating function of the dance is primitive; but this seems most unlikely, since food-finding is a frequent event, but nest-finding very rarely, if ever, occurs more than once in the life of any worker. If the food-finding function is primitive, it is quite intelligible that a prelude to outward flight under the influence of one drive should come to be associated with outward flight under the influence of another. It seems that a dance is only performed when a bee "intends" to fly to a definite place under the influence of a sufficiently strong drive. It is not apparently performed before a searching flight, and LINDAUER's observations on nest site indication support the view that it usually predicts the extrusion of the scent organ.

Among the ancestors of the hive bee new nests were presumably founded by fertilized queens unaccompanied by workers. The queens therefore did all the searching. The development of sociotomy, that is to say the splitting of a large community, was an important evolutionary step. It was presumably made possible by the transfer of the site-searching drive from queens to workers, and the association of dancing with this drive. Once again these changes may have occurred gradually. A tendency for even a few workers to accompany a migrating queen would have been advantageous. So would a tendency for workers to perform the arduous and dangerous duty of searching for a nest site.

It is clear, however, that the study of the evolution of the dance demands observations on a number of species, as well as on the various races of *Apis mellifera*. The most important single step in this evolution may have been the establishment of connexions between the centres concerned in flying and walking. These may even, like the connexion between the human brain centres controlling the right hand and the speech muscles, be capable of discovery by anatomical methods.

DISCUSSION

The bees' dances are an intraspecific communication unlearned on both the motor and sensory sides (von FRISCH, 1952). They are therefore social releasers according to THORPE's (1951) definition. But they certainly do not agree with the criterion of LORENZ and TINBERGEN (1939) who stated that "die Form der ausgelösten Bewegungen von derjenigen der auslösenden Reize unabhängig ist". These authors have later adopted a less rigid attitude, but still seem to regard it as unusual that taxis components in the response should be determined by the form of the releaser. Their statement is of course true about the round dance.

We have argued both that bees' dances have the function typical of social releasers, which is to evoke in partners behaviour harmonious with the future behaviour of the actor; and also that they could have had an evolutionary history similar to that hypothesised for other social releasers. They resemble simpler social releasers in being complicated spatial and temporal patterns (1). However, as a waggle cannot be made without indicating a direction, the orientating or taxis component adjusting to the spatial environment is integral to the releaser. This taxis component also includes information abstracted from considerable periods of the past, and directs the behaviour which it releases.

The taxis component of vertebrate releasers is often similarly elaborate. A male of the Rassenkreis *Triturus cristatus*, while walking away from the female leading her during their courtship, both before and after depositing his spermatophore, repeatedly turns his head to look at the female. He adjusts his route according to the direction of her gaze, but with considerable prevision of the obstacles and boundaries of their aquarium. If the angle at which her head points diverges too far from his path, he turns and recourts with tail-wagging and lungeing movements, whether or not the spermatophore has left his cloaca.

In mammals there seems to be an evolutionary trend, comparable to but different from that in the Hymenoptera, increasing the importance of taxis components relative to fixed action patterns (McDOUGALL, 1928). The capacity for variation in form of movement seems to be the locomotory specialization of this group, quite as typical as the locomotory specializations that characterise Aves, Serpentes and Salientia (MAYNARD SMITH and SAVAGE, 1954). This trend has culminated in man, in whom no fixed action patterns of skeletal muscular movement can be observed. For this reason we protest against HINDE's (1953, *b*) description of a consummatory act as one "in which only one motor pattern is possible".

Without supporting PAGET's (1930) and JOHANNESSON's (1949) theory that human speech arose by a deliberate imitation with the mouth of

(1) This is not a universal property of sign stimuli. The chemical sign stimuli for human breathing are provided by the mass of O₂ and CO₂ present in a given volume, not by the percentage composition of the gas mixture breathed (HALDANE and PRIESTLEY, 1935).

manual and other gestures, we think that it may well contain components kinaesthetically equivalent with other bodily movements, in the same way as a vertical run is kinaesthetically equivalent with a bee's flight towards the sun.

But the bees' dances can better be compared with a human communication which is largely kinaesthetic, and has non-human equivalents. Copulation is an exchange of tactile and kinaesthetic releasers. These evoke ejaculation, and perhaps even ovulation (CAMPBELL & PETERSEN, 1953). The former is the type (in the taxonomic sense) of a consummatory act; the word "consummation", chosen by SHERRINGTON (1906) and CRAIG (1918), has a sexual meaning in English legal terminology.

Male mammalian pelvic thrusts, though a spinal reflex, are not a fixed action pattern in man, since they are absent in vacuum activity (the only vacuum activity which has a name in common speech) and in some copulatory positions. Many female mammals make pelvic thrusts under the influence of the reproductive drive, but they are mechanically impossible in many species during copulation. Many women make them during copulation. McDougall's consideration about vocalisation apply to them. The sensory "feed-back" from pelvic thrusts is the same whichever sexual partner performs them. Such a perceptual identity of sensory stimuli, whether derived from the partner or actor, may be a necessary condition for imitation. This would explain why animals so rarely imitate elaborate muscular movements. They can only be expected to imitate movements seen by themselves if they can see the parts of their own bodies moved in imitation.

A woman, when imitating this male pelvic thrusting "without previous experience... responds to a biologically relevant situation with specific behaviour of indubitable survival value" (LORENZ, 1951, p. 160) and her behaviour fulfils all the criteria which TINBERGEN (1951, p. 51-54, 142-150) requires for his usage of the adjective "innate". However we know that this item of behaviour is very variable both between cultures and between individuals of the same culture. Its ontogeny (ethogenesis) in an individual may be due to any of a number of "learning" processes. These include "imitation", instruction, and discovery for oneself in a manner comparable to a dove's discovery of the sensations of a nest box (CRAIG, 1918). We also know that its neural connexions differ, as shown by its association with the speech mechanism, its capacity to lead to a consummation, and the different motor patterns of this orgasm. We know that it varies as a result of social conditioning (Aristophanes, *Lysistrata*; Lucretius, *De rerum natura*): we do not know whether any of its variation is genetically determined. We suggest that most of the above considerations apply, *mutatis mutandis*, to bees' dances, and that the comparable but quite different trends in the two phyla raise fundamental considerations as to how behaviour changes occur in evolution.

We agree with SPALDING (1873) that patterns of behaviour can be learnt in ancestors and unlearnt in their descendants, just as morphological

structures may only arise in ancestors in response to specific stimuli, but yet arise in their descendants in most environments compatible with life (see SIMPSON, 1953, and WADDINGTON, 1953, *a* and *b*). The strongest evidence that this is a common evolutionary sequence is provided by students of the adaptive habitus of plants, who use methods comparable to those of ethologists, and are developing a vocabulary (THODAY, 1953) which avoids the inconsistencies which HEBB (1953) has pointed out in ethological vocabulary. SPALDING (1873) compared the epigenetic and evolutionary processes by which behaviour patterns and structures change. It seems likely that evolutionary changes in behaviour, including changes in the various components of an instinct (1), would be described by an ethologist as learning (1) processes in individual animals.

A conditioned reflex or a learned habit is presumably represented by some change in the central nervous system. Some of these changes may be so complicated that the genetic potentialities of a species will not suffice, during the time available for evolution, to emancipate them from environmental conditions subjectively called "practice" and "experience". Those attributes of an animal which are interpreted as having been evolved to provide the key stimuli for innate releasing mechanisms resemble, in their simplicity and improbability, the patterns called warning colorations, associated with "unpleasant" smells, tastes, and stings. These latter are adaptations to produce a rapid and stable negative conditioning (MOSTLER, 1935). Such negative conditioning is distinguished from an innate releasing mechanism by the same methods as an ecophene is distinguished from an ecotype (TURESSON, 1922, SPURWAY, 1955); and we suggest that they are related to one another in the same way. The neural changes of negative conditioning are easily produced and are probably simple. The selective advantage of euryphagy, in the sense of attempting to eat a wide range of objects, must be reversed only in very special circumstances. Hence segregating genotypes which make the epigenetics of recognition of these warning signals independent of environmental influences (WADDINGTON, 1953, *a* and *b*, and earlier) have rarely been selected. SPALDING (1873) found that some chicks of the domestic fowl never pecked at wasps. It thus appears that the epigenetics are sometimes genetically assimilated in a population which is being selected not to exercise choice as to food (DECHAMBRE, 1941, HEDIGER, 1950, SPURWAY, 1955), but to accept what it is given. The generalised selective advantage of euryphagy may explain why few species have evolved innate releasing mechanisms to be released by poisons, as they have evolved those which are released by predators and by salt water.

(1) The grammatical structure of many languages leads to the following unjustifiable assumptions:

"Instinct" is a noun and therefore a thing, and it is profitable to look for its invariable material basis.

"Learning" is a participle and therefore a process, both changing and changeable, so a "lesson" need not have an invariable material basis in the nervous system.

The number of generations during which a learned ethogenesis evolves into an instinctive ethogenesis, if it does so at all, depends on the relative strength of the selection pressures favouring uniformity and variability in development. The song of domestic canaries seems to have become less and less learnt during 167 years (BARRINGTON, 1773, METFESSEL, 1940), though no similar trend in the songs of the wild species with which they form hybrids has been observed. This difference presumably depends on the changed function of song in a male canary; his chance of obtaining a mate still depends on his prowess as a singer, but no longer, as in wild finches, on his efficiency in holding a territory. PROMPTOV (1944) discussed why the territorial function is best served by ontogenetic plasticity.

JAMES' (1891) "law of the inhibition of instinct by habits" seems to refer to an intermediate stage in the evolutionary process which we postulate. The neural connexions associated with the perception of some stimuli provided by a potential partner appear to be independent of environmental influence. But other neural connexions are very rapidly evoked by a wide range of external objects during a limited period of ontogeny without obvious reinforcement (SPALDING, 1873). But the external stimuli for this rapid ethogenesis are not so simple as those which provide the indifferent stimulus for a conditioned reflex of Type I, or act as sign stimuli for an innate releasing mechanism (LORENZ, 1951 and earlier). BOYD and FABRICIUS (1954 and personal communication by Dr. FABRICIUS) found that the reactions of baby ducks (*Anas platyrhynchos*) were stabler towards an appropriately behaving female than towards substitutes. Similarly PROMPTOV (1944) found that birds learn the song of their own species more rapidly than alternatives, and select it from among various sounds which they hear. A habit in James' sense is both a subordination of sign stimuli and a response to features of the environment apparently different from those which act as indifferent stimuli for a conditioned reflex type I.

During metazoan evolution the genes (*sensu lato*) are the organs least influenced by the environment during ontogeny, while the nervous system is the organ most specialized to be so influenced. So it is hard to imagine agents which select between genotypes, which would not also, and more rapidly, produce adaptive effects in somatic tissue, including the nervous tissue. However, the more nearly an environment imposes an "all or none" Darwinian fitness, and the more abruptly the conditions of fitness have been altered, the more it will tend to select phenotypes rather than induce nervous change. Under such conditions we might say that if individuals are given no time to learn, only psychopaths will survive (SPURWAY, 1955). Such environments must rarely occur except as recent human artefacts. When they occur, for example when a winged species of insect colonises a small oceanic island, we may expect instincts or structures to be abruptly lost, rather than gradually adapted.

The hypothesis that instinctive behaviour will rarely change unless the members of the ancestral population have made comparable changes

in their behaviour as a result of environmental exigencies (SPALDING, 1873) provides a possible answer to TINBERGEN's (1953, p. 234) question as to how responsiveness of the reactor to a signal is evolved. Assuming that mutual activity is advantageous and (where such a word is applicable) pleasurable to both animals concerned, the signal could, for a number of generations, be the repeatedly conditioned indifferent stimulus for a conditioned reflex type I. Similarly the essential part of ritualization—the invariable association of two movements—could come about if for some generations the movement resulting from conflict provided the proprioceptive stimulus for a conditioned reflex type II. It is important to remember that the psychological contexts which BASTOCK, MORRIS, and MOYNIHAN (1953) describe as conflict and thwarting are identical with the experimental conditions necessary to produce a type II conditioned reflex (KONORSKI, 1948, p. 235-237). Professor R. W. RUSSELL tells us that conditioned reflexes type II are harder to extinguish than type I. This provides confirmation for the LANGE-JAMES theory of emotion and for our dependent suggestion about the evolutionary advantages of preludes.

The ancestors of the bees which dance and respond to dances, the queens and drones, do not perform these activities, though very rarely a drone developing from a worker's egg may become an ancestor. Hence, as DARWIN (1878) pointed out, a Lamarkian or Michurinian explanation of the bees' communicatory system is impossible. However, selection based on the performance of relatives is known to be effective. Cattle have been effectively selected for high milk yield and high butter content of their milk. This has been done not, in the main, by breeding from cows whose milking record was satisfactory, but from bulls whose mothers, sisters, and daughters were good milkers. Similarly some breeds of horses are preferred largely on the basis of the performance of male castrates.

Natural selection on bees presents peculiar, but favourable, features. The workers within a hive are of different genotypes. Von FRISCH (1952) insists on the importance of individual differences in behaviour between workers. If these are genetically determined, they depend on the heterozygosity of the queen and would disappear as the result of prolonged inbreeding. A new gene in the father of a hive would be present in all the workers and none of the drones, but it would only be present in half the workers of hives founded by his daughters. On the other hand only genetic changes due to mutations late in the germ line of either parent can cause isolated occurrences of aberrant animals. In most animal species an abnormal type of behaviour, however determined, must usually be a handicap because it tends to hinder the animal manifesting it from taking part in social activities, including sexual activities. In hive bees and other social Hymenoptera genetic variation, including segregation of genotypes, will usually occur in several sisters, so that changes in reaction need not hinder cooperation. There is no natural selection imposed by the necessity of adjustment to a sexual partner. On the other hand, any deviants in the

anthropological sense that are able to contribute to the well being of the hive are increasing the number of the swarms produced, and therefore the fertility of their sexual sisters (DARWIN, 1878), among whom the alleles or combination of alleles segregated in exactly the same frequency. A similar situation will occur in the termites with slightly different details because both sexes are diploid.

This assumes that in both groups a genetic change in one caste need not be penetrant in another caste, even though the caste differentiation is due to environmental agencies. This is what we would expect from a study of insect morphogenesis. Genes altering the development of the legs of *Drosophila melanogaster* do not influence the development of the *aristae*, which arise from serially homologous imaginal discs. Stocks of this species can be obtained in which environmental changes determine whether the *aristae* are normal or leg-like. If conditions are adjusted so that the *aristae* are leg-like, they now show the leg phenotype appropriate to the genotype of the stock (BRAUN, 1940).

It is possible that the constructional and communicatory capacities of the social insects, and of man, have arisen because these three groups have evolved social organisations which permit non-reproducing members of a community to contribute to the Darwinian fitness of animals having similar genotypes to themselves. This reduces the effect on the species of the various conservative actions of natural selection.

The caste systems of human societies differ from those of the social insects, because in the former there is reduced gene interchange between the groups serving different social function. Division of labour without exogamy between individuals with the various specializations gravely reduces the exploitation of genetic variation by the population as a whole.

This paper contains many speculations which may be useful even if untrue, because they can be confirmed or disproved by straightforward observation and experiment. For example equation (2) or Fig. 1 enable us to calculate that a flight to a distance of 2 kilometers should be predicted by a dance with 28 waggles per straight run. This may well be as incorrect as similar extrapolations in physics have proved to be. Again the accuracy of the mean direction and distance may prove to be, on the whole, greater or less than in the three observations cited. If we had the possibility of working with bees we should naturally have postponed publication until our own observations gave us at least some indication of the truth or falsity of such hypotheses. As we have no such possibility, we hope that other workers will test them.

Our opinions as to evolutionary processes cannot be confirmed or disproved so quickly. A satisfactory evolutionary theory can only be reached by testing a variety of hypotheses both for agreement with known facts and for logical consistency. The hypotheses of workers like ourselves who have come to the problem of evolution mainly from a study of genetics are bound to differ from those of workers whose experience has been mainly in the fields of palaeontology, taxonomy, or ethology.

Summary.

An analysis of von FRISCH's data yields the following results. In two experiments the direction taken by the central bee in a group directed to a goal deviated by $2-3^{\circ}$ from the correct direction. This error could be due to the earth's rotation. The standard deviations of directions round this mean were about 14° . In one experiment the error of the central bee in distance was about $+5\%$, the standard deviation probably about 30% . The dance conveys about 5 cybernetic units of information concerning direction, of which the average recipient receives at least 2.5.

Between 100 and 3,000 metres the number of turns made in a given time falls off linearly with the logarithm of the distance. At greater distances it falls off more slowly. The number of abdominal waggles made per straight run increases by 1 per 75 metres between 100 and 700 metres. It is suggested that this is the principal means by which distance is communicated.

The dance is seen as a highly ritualized intention movement leading to communication which is mainly kinaesthetic. The bees which are sent out by the dance fly to the appropriate goal because, by following the dancer, they have automatically carried out the intention movements for the flight. The same principle applies to other communications in which the signal is repeated, including many bird calls.

Bees' communication resembles that of an analogical calculator such as a slide rule, while human language resembles that of a digital calculator such as an abacus or a desk machine. A bee's dance may be regarded as a propositional function with four variables.

An evolutionary history of the dance is suggested, beginning with dances such as the round dance which merely alert other bees, and gradually acquiring a directive character as the populations of hives increased. The movements of a pointer dog suggest how a directional dance may have started. Suggestions are made as to the possible neurological basis of communication.

The bee dances correspond with social releasers in their patterns of motor and sensory ontogeny, and their function in the economy of the species. The waggle dance, however, shows a hypertrophy of the component orienting to special features of the environment. A similar trend exaggerating the taxis component occurs in the Mammalia, and culminates in man, in whom fixed action patterns of skeletal muscular movement do not exist. Such trends are comprehensible if we assume evolutionary change to proceed by learnt changes in behaviour. The development of a small proportion of these changes becomes, during phylogeny, independent of environmental influences. What variations of behaviour thus become instinctive will depend both on the genetic potentialities of the species, and on the selection pressures in favour of invariability. A Lamarckian explanation of bee dances is particularly difficult. But

insect communities descended from a single pair offer very favourable opportunities for natural selection (1).

Sommaire.

L'analyse des données de VON FRISCH conduit aux résultats suivants. Dans deux expériences, la direction prise par l'Abeille centrale d'un groupe dirigé vers un but a dévié de 2° à 3° de la direction correcte. Cette déviation pourrait s'expliquer par la rotation de la terre. L'écart type des directions autour de ce moyen était à peu près 14°. Dans une expérience, l'erreur de distance de l'Abeille centrale était moins que 1 p. 100 : l'écart type était 13 p. 100 à peu près.

La danse transmet environ 5 unités cybernétiques d'information sur la direction, dont l'Abeille moyenne reçoit au moins 2,5.

Entre 100 et 3 000 mètres, le nombre de tours fait en un temps donné décroît en fonction linéaire du logarithme de la distance. A de plus grandes distances, il décroît plus lentement. Entre 100 et 700 mètres, le nombre d'oscillations abdominales pour chaque cours en ligne droite monte par 1 pour 75 mètres. Nous suggérons que c'est là le moyen principal de communication de distance.

Nous voyons la danse comme un mouvement d'intention hautement ritualisé, conduisant à une communication surtout kinesthétique. Les Abeilles émises par une danse volent au but indiqué, parce qu'en suivant la danseuse elles ont automatiquement fait les mouvements d'intention pour le vol. Le même principe s'applique aux autres communications dans lesquels un signal se répète, y compris maints cris d'oiseaux.

La communication des Abeilles rappelle celle d'un calculateur analogique, comme la règle à calculer, tandis que la langue humaine ressemble à la communication d'un abaque ou d'une machine de bureau. On pourrait décrire une danse d'Abeilles comme une fonction propositionnelle à quatre variables.

Nous suggérons une histoire évolutionnaire de la danse, qui aurait commencé par des danses comme la danse en ronde, ne servant qu'à alerter les autres Abeilles, et qui aurait lentement acquis un caractère directif à mesure que la population des ruches s'augmentait. La danse directionnelle aurait pu commencer par des mouvements comme ceux d'un Chien de chasse pointer. On discute des bases neurologiques possibles de la communication.

Les danses des Abeilles correspondent aux déclencheurs sociaux dans leurs ontogénies motrices et sensorielles et dans leur fonction écono-

(1) „In *Aus dem Leben der Bienen* (Berlin, 1953) von FRISCH gives another experiment on the accuracy of communication of distance. Here the correct distance was 2 000 metres. Using the same methods as with Table 5, the errors of the mean bee were + 5 and — 9 metres. The standard errors were 248-274 and 261-303 metres. Thus these data indicate more accurate communication than those of Table 5.”

mique. Mais la danse oscillatoire décèle une hypertrophie du component orientée vers des propriétés spéciales du milieu. Chez les Mammifères, une tendance semblable, exagératrice du component du taxis, aboutit à la conduite humaine, où l'on ne trouve pas de formes à déterminisme endogène dans le mouvement des muscles volontaires. De telles tendances deviennent intelligibles si les changements évolutionnaires s'accomplissent au moyen des changements appris dans le comportement.

Le développement d'une petite fraction de ces changements devient, pendant la phylogénie, indépendant des influences extérieures. C'est à la fois les potentialités génétiques d'une espèce et les pressions sélectrices favorisant la fixité qui déterminent quelles sont les variations du comportement, qui deviennent ainsi instinctives. Une explication lamarkienne des danses des Abeilles est bien difficile. Mais les communautés d'insectes descendues d'une même paire offrent des conditions très favorables à la sélection naturelle.

Zusammenfassung.

Eine Analyse von Von FRISCH's Ergebnissen gibt die folgenden Resultate. In zwei Experimenten wich die Richtung, die die mittlere Biene in einer Gruppe die einem betreffenden Ziel zustrebte um 2° - 3° von der richtigen Richtung ab. Diese Abweichung könnte durch die Erddrehung verursacht sein. Die mittleren quadratischen Streuungen um diesen Mittelwert der Richtungen betrugen durchschnittlich circa 14° . Was die Distanz anbelangt, so war in einem Experiment die Abweichung der mittleren Biene ungefähr 1 %, mit einer Streuung von wahrscheinlich circa 13 %. Ein Tanz der sich an Richtungsmitteilungen betrifft, übermittelt ungefähr 5 cybernetische Einheiten, von denen ein Durchschnittsempfänger mindestens 2,5 Einheiten aufnimmt. Von 100 zu 3 000 Metern fällt die Anzahl von Drehungen, die während einer bestimmten Zeit ausgeführt werden, linear mit dem Logarithmus der Entfernung. Bei größeren Entfernungen fällt sie langsamer. Die Anzahl der Schwänzelbewegungen mit dem Abdomen während einem Lauf geradeaus nimmt in Grenzen zwischen 100 und 700 Metern um eine Bewegung für jede 75 Meter zu. Es wird nahegelegt daß dies die Hauptmethode für die Mitteilung der Distanzen ist.

Der Tanz erscheint als eine in hohem Maße ritualisierte Intentionsbewegung, die zu einer hauptsächlich kinästhetischen Verständigungsweise führt. Bienen, die durch diesen Tanz ausgesandt werden, fliegen deshalb zu dem betreffenden Ziel weil sie, wenn sie dem Tänzer folgen, automatisch die Intentionsbewegungen für diesen Flug ausgeführt haben. Dasselbe Prinzip trifft auch für andere Mitteilungen zu, in denen ein Signal wiederholt wird, so auch für viele Vogelrufe.

Die Verständigung zwischen Bienen ähnelt der einer analogen Rechenmaschine, zum Beispiel einem Rechenschieber, während die

menschliche Sprache der einer zahlenmässigen Rechenmaschine, wie zum Beispiel einem Abakus oder einer Büromaschine, ähnelt. Einen Bientanz kann man als eine Satzfunktion mit vier Variabeln betrachten.

Eine Evolutionsgeschichte des Tanzes wird vorgeschlagen, beginnend mit Tänzen wie die Rundtänze die bloss andere Bienen alarmieren, und allmählich einen bestimmenden Character annehmen wenn die Bevölkerungen der Bienenstöcke anwuchs. Die Bewegungen eines Pointerhundes legen nahe wie die Richtungstänze begonnen haben mögen. Es werden Vorschläge für eine mögliche neurologische Basis der Verständigung gemacht.

Die Bientänze entsprechen in der Art ihrer motorischen und sensorischen Entwicklung und in ihrer Funktion in der Wirtschaft der Spezies sozialen Auslösern. Der Schwänzeltanz zeigt jedoch eine Ueberentwicklung desjenigen Komponenten, der zu bestimmten Eigenschaften der Umgebung hingewendet ist. Eine ähnliche Entwicklung mit dem Hauptgewicht auf dem Taxiskomponenten kommt bei Säugetieren vor, und erreicht ihren Höhepunkt beim Menschen, bei dem ein bestimmtes Aktionsmuster für Willkürbewegungen der Skelettmuskulatur nicht besteht. Solche Entwicklungsrichtungen sind verstehbar wenn wir annehmen, daß entwicklungsgeschichtliche Änderungen durch erlernte Änderungen in der Verhaltensweise vorkommen. Die Entwicklung eines geringen Teiles dieser Änderungen wird im Laufe der Phylogenie unabhängig von Umgebungseinflüssen. Welche Variationen der Verhaltensweise schliesslich instinktiv werden, wird von den genetischen Möglichkeiten sowohl als von dem Selektionsdruck in Richtung auf Unveränderlichkeit hin abhängen. Eine Erklärung des Bientanzes auf der Basis von Lamarck ist ganz besonders schwierig. Aber Insektengemeinschaften, die von einem einzelnen Paar abstammen, bieten besonders günstige Gelegenheiten für natürliche Auslese.

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UNTERSUCHUNGEN UEBER DEN NÆHRWERT VON POLLENERSATZMITTELN FUER DIE HONIGBIENE (I)

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Ziel meiner 1950 begonnenen Untersuchungen ist es, die heute bekannten, in ihrer Brauchbarkeit für die imkerliche Praxis noch immer unterschiedlich beurteilten Pollenersatzmittel auf ihren Nährwert für die Biene und ihre brutanregende Wirkung zu untersuchen und sie in einem möglichst vielseitigen Prüfverfahren untereinander und mit Naturpollen in Vergleich zu setzen. Bisherige Untersucher von Pollenersatzmitteln, deren Ergebnisse im Rahmen dieses kurzen Berichtes nicht erörtert werden können, beschränkten sich meist auf einen oder wenige Tests, in der Mehrzahl auf die Ausbildung der Pharynxdrüsen oder anderer in ihrer Entwicklung von der Pollennahrung abhängiger Organe oder auf den Stickstoffgehalt der Versuchsbienen als Maß für die Assimilierbarkeit der verfütterten Eiweißmittel. Meine Absicht war es, möglichst viele Tests für die Prüfung der Ersatzmittel heranzuziehen, um damit zugleich ein Urteil über den Wert der verschiedenen Tests zu erhalten. Darüber hinaus erhoffte ich mir durch den Vergleich von Pollenersatzmitteln unterschiedlicher Zusammensetzung und ihrer Wirkung bei verschiedenartigen Tests einen Einblick in den Eiweiß- und Vitaminstoffwechsel der Biene.

Als Tests dienen die Ausbildung der Pharynxdrüsen, des Eiweiß-Fettkörpers und der Ovarien der Arbeitsbiene, ergänzt durch mikrochemische Stickstoffbestimmungen, die Lebensdauer gekäfigter, bei Stocktemperatur im Thermostat gehaltener Bienen, die Brutfähigkeit von Völkern unter Abschluss von der natürlichen Tracht und die Überwinterungsfähigkeit von Bienenvölkern. Für alle Tests werden die Versuchsbienen aus pollenfreien Brutwaben im Thermostat gewonnen und vom Schlüpfen ab neben Zuckerkost entweder ausschliesslich mit den zu prüfenden Ersatzmitteln oder zum Vergleich mit Naturpollen verschiedener Art ernährt. Als Kontrollen dienen nur mit Zucker gefütterte Bienen aus dem gleichen Schlupf. Zur endgültigen Beurteilung des Wertes der Pollenersatzmittel schien es mir ferner erforderlich, mit Ersatzmitteln erbrütete Bienen auf ihre Lebensdauer und ihre weitere Brutfähigkeit zu untersuchen.

Geprüft wurden bisher folgende Ersatzmittel: Waldhof-Höselhefe

(1) Vorläufige Mitteilung nach einem am 4.8.53 auf der Tagung der Deutschen Sektion der Union in Hamburg gehaltenen Vortrag.

(Torula-Hefe), die neuerdings von GONTARSKI (1948, 1950, 1951, 1954) empfohlen wird, Bierhefe, Vollsojamehle verschiedener Herkunft, mit Kohlenwasserstoffen entfettetes Sojamehl (sog. Bäckersojamehl), welches in den Jahren 1948 und 1949 als Pollenersatzmittel an die deutsche Imkerschaft ausgegeben wurde, und ein aus mechanisch teilweise entfettetem Sojamehl und Bierhefe hergestelltes Präparat. Zur Prüfung noch vorgesehen sind Trockenmilch und je nach dem weiteren Verlauf der Untersuchungen Gemische der verschiedenen Ersatzmittel.

Um für die Ausbildung der Pharynxdrüsen einfache Zahlen zu erhalten, welche die Berechnung von Mittelwerten und deren statistische Sicherung erlauben, wurde die Grösse der Drüsenbeeren bei verschiedener Ernährung mikrometrisch gemessen. Je Fütterungsart einer Serie wurden 100 Bienen untersucht, je Drüse einer Biene 50 Acini nach Länge und Breite gemessen. Die erhaltenen Grössenunterschiede bei grundlegend verschiedener Ernährung sind statistisch gesichert, die Werte bei gleicher Fütterung stimmen in verschiedenen Serien gut überein, sodass die Methode als brauchbar angesehen werden kann. Die grössten Drüsenbeeren im Mittel der untersuchten Bienen zeigten in den bisherigen Versuchen die mit Pollen ernährten Tiere, auch wenn handgesammelter Pollen mit ebenfalls von den Bienen unverarbeiteten Ersatzmitteln verglichen wurde. Die kleinsten Drüsenbeeren wiesen erwartungsgemäss die nur mit Zucker ernährten Kontrolltiere auf. Die Drüsen frisch geschlüpfter Bienen liegen zwischen diesen Extremen; die Unterschiede sind nach beiden Seiten statistisch gesichert. Dem Pollen am nächsten kam in den bisherigen Versuchen Bierhefe, in einer Versuchsreihe auch ein Vollsojapräparat Schweizer Herkunft (Unterschiede zu Pollen nicht mehr gesichert), doch liegt auch die Drüsengrösse der mit anderen Vollsojamehlen oder Torula-Hefe ernährten Tiere weit über der frisch geschlüpfter Bienen. Dagegen waren die Drüsen der mit Bäckersojamehl gefütterten Bienen fast ebenso unentwickelt wie die von Zuckerbienen. Alle bisherigen Ergebnisse wurden an fixierten Drüsen gewonnen. Sie müssen noch durch Messungen an frisch präparierten Drüsen und durch histologische oder physiologische Prüfung der Futtersaftsekretion ergänzt werden. Im besonderen bleibt zu untersuchen, ob geringen Grössenunterschieden der Drüsenbeeren, auch wenn sie metrisch gesichert sind, eine funktionelle Bedeutung zukommt.

Die Ergebnisse der mikrochemischen Stickstoffbestimmung von Köpfen stehen in gutem Einklang mit den Drüsenmessungen. Die präparative Untersuchung des Eiweiß-Fettkörpers ist noch nicht abgeschlossen, dagegen brachten die mikrochemischen Stickstoffbestimmungen von Hinterleibern analoge Ergebnisse zu den Unterschieden im Stickstoffgehalt der Köpfe.

Die Aktivierung der Ovarien von Arbeitsbienen wurde bisher nur physiologisch geprüft, indem kleine Völkchen aus weisellosen Bienen bei ausreichender Ernährung mit Pollen oder Ersatzmitteln und bei Bruttemperatur im Thermostat gehalten wurden. Es ergab sich, gemessen

an der Zahl der abgelegten Afterweisel-Eier und der erbrüteten Drohnen, eine deutliche Ueberlegenheit der mit Mischungen aus Bienenbrot oder Pollenhöschchen ernährten Bienen gegenüber den Ersatzmitteln. Diese waren aber handgesammeltem Haselpollen etwa gleichwertig.

Der Testwert der Lebensdauerversuche beruht auf den Befunden von BEUTLER und OPFINGER (1949) und MAURIZIO (1946, 1950, 1951) über die lebensverlängernde Wirkung des Pollens. Ich habe bei diesen Versuchen den Pollen und die zu vergleichenden Ersatzmittel teils in Mischung mit Honig oder künstlichem Invertzucker zur Wahl neben Zuckerteig, teils in verschiedener Konzentration unmittelbar im Zuckerteig verfüttert. Die Ergebnisse beider Methoden stimmen im Wesentlichen überein. Bei Verfütterung von Pollengemischen in Form von Bienenbrot oder Pollenhöschchen war die lebensverlängernde Wirkung des Pollens grösser als aller bisher geprüften Ersatzmittel. Die mittlere Lebensdauer der mit Ersatzmitteln—ausser Bäckersojamehl—ernährten Bienen lag jedoch weit und statistisch hoch gesichert über der Lebensdauer der mit Zucker ernährten Kontrolltiere. In guter Übereinstimmung mit den Ergebnissen der Drüsenmessungen zeigte Bäckersojamehl bei Verfütterung zur Wahl neben Zuckerteig keine, bei Verfütterung im Zuckerteig eine nur geringe lebensverlängernde Wirkung gegenüber reiner Zuckernahrung. Dem Pollen am nächsten kamen im Mittel der bisherigen Versuche Bierhefe und das aus Sojamehl und Bierhefe hergestellte Präparat. Torulahefe war in einem Teil der Versuche den Vollsojamehlen ebenbürtig, in manchen Versuchen jedoch deutlich und statistisch gesichert unterlegen. Auch bei Versuchen, bei denen sich die Bienen durch eingeschaltete Fluggelegenheit in Flugkisten nach BÖTTCHER (1948), Flugzelten oder unter kontrollierten Bedingungen im Freien regelmässig entleeren konnten, blieben die Ergebnisse unverändert. Da die vitaminreiche Torula-Hefe bei anderen Testen, im besonderen der Brutfähigkeit, den Sojapräparaten mindestens gleichwertig ist, wurde vermutet, dass für die Lebensdauer nur der Eiweißgehalt, für die Ausbildung der Pharynxdrüsen und das Brutvermögen ausserdem der Vitamingehalt der Futtermittel ausschlaggebend ist. Diese Frage wird z. Zt. von Frl. cand. zool. Back an unserem Institut gesondert verfolgt. Die bisherigen Ergebnisse machen die geäußerte Vermutung wahrscheinlich und stehen damit in Übereinstimmung mit den Ergebnissen von PAIN (1951, 1954) über den Einfluss der Vitamine auf die Ausbildung der Ovarien von Arbeitsbienen.

Die lebensverlängernde Wirkung von handgesammeltem Haselpollen war im Mittel der bisherigen Versuche nicht grösser als die der Ersatzmittel. Diese Unterlegenheit von handgesammeltem Pollen gegenüber den Mischungen aus Bienenbrot oder Pollenhöschchen glaubte ich in meinem Vortrage so deuten zu dürfen, dass von den Bienen verarbeiteter Pollen wirksamer sei als handgesammelter Blütenstaub. Hierin bestärkten mich die Ergebnisse von BEUTLER und OPFINGER (1949). Inzwischen durchgeführte, technisch allerdings noch unbefriedigende Kontrollversuche, bei denen die lebensverlängernde Wirkung von gehöseltem und hand-

gesammeltem Hasel- und Erlenpollen verglichen wurde, bestätigten diese Deutung nicht, dagegen war gehöselter Hasel- und Erlenpollen anderen gehöselten Pollenarten, z.B. von Raps und Löwenzahn, unterlegen. Dies entspricht den Befunden von MAURIZIO (1950), die ebenfalls eine unterschiedliche Wirksamkeit verschiedener Pollenarten auf den physiologischen Zustand und die Lebensdauer von Bienen festgestellt hat. Damit ist ein genereller Vergleich zwischen Naturpollen und Ersatzmitteln, wie ich ihn ursprünglich anstrebte, nicht möglich. Ziel der weiteren Versuche muss es sein, die Ersatzmittel mit verschiedenen Pollenarten in jeweils gleichen Zustandsformen (gehösel oder unverarbeitet) zu vergleichen. Nach Vorversuchen, welche ich im Herbst und Winter 1953 vornahm, scheint Vollsojamehl in der lebensverlängernden Wirkung Löwenzahnpollen etwa gleichzukommen, ist Hasel- und Erlenpollen gering und Kiefernpollen deutlich überlegen, erreicht aber nicht die Wirkung von Rapspollen.

Zur Untersuchung der Brutfähigkeit wurden gleich starke Völkchen von 1200 bis 1500 Bienen in Einwabenkästchen aus pollenfrei geschlüpften Jungbienen gebildet und in Flugzelten aufgestellt. Die zu prüfenden Ersatzmittel, bezw. Pollen wurden in Mischung mit Honig (in besonderen Kontrollen in Mischung mit künstlichem Invertzucker) in die Wabe eingeschleudert. Ausserdem wurden die Völkchen reichlich mit Zuckerwasser gefüttert und in den ersten Tagen beweiselt. 20 Tage nach Beginn der Eiablage, d.h. unmittelbar vor dem Schlupf der ältesten Brut, wurde der Brutansatz ausgezählt und die gedeckelte Brut zur Registrierung des Schlupfes und weiteren Verwendung der Jungbienen in einen Brutschrank gestellt. Alle mit Bierhefe, Torula-Hefe und Vollsojamehlen gefütterten Völkchen gingen überraschend gut und meist ohne Verzögerung gegenüber den Pollenvölkchen in Brut und brachten die Larven normal zur Puppenreife. Auch der Schlupf der verdeckelten Brut war prozentual nicht schlechter als bei den Pollenvölkchen, doch erzielte bisher keines der geprüften Ersatzmittel einen ebenso hohen Brutansatz wie natürliche Pollengemische aus Bienenbrot oder Pollenhöschchen. Bei dem Vergleich der Pollenersatzmittel untereinander zeigte bisher Bierhefe den besten Bruteffekt. Torula-Hefe war den Sojamehlpräparaten etwas überlegen. Da jeder Versuch mit der Bildung der Völkchen etwa 4 Wochen dauert, Brutversuche nur während kurzer Zeit im Jahre durchführbar sind und mir zunächst nur zwei, seit einem Jahr vier Flugzelte zur Verfügung stehen, ist die Zahl der Versuche aber noch zu klein, als dass die festgestellten Unterschiede zwischen den verschiedenen Pollenersatzmitteln schon als gesichert angesehen werden könnten. Ich habe deshalb grosse Mühe darauf verwandt, Brutversuche mit kleinen, im Thermostat gehaltenen Modellvölkchen durchzuführen, denen regelmässig Fluggelegenheit in Flugkisten, Flugzelten oder im Freien gegeben wurde. Die Ergebnisse waren leider unbefriedigend. Bemerkenswert erscheint mir aber, dass unter diesen unnatürlichen Bedingungen regelmässig nur die mit Pollengemischen und nur in seltenen Ausnahmefällen die mit Ersatzmitteln gefütterten Völkchen Brut bis zum Verdeckeln brachten. Die

Lärvcchen verschwanden spätestens am 3. Lebenstag, meist schon früher. Auch mit handgesammeltem und gehöseltem Hasel- und Erlenpollen brüteten die Völkchen unter diesen Bedingungen nicht. In guter Übereinstimmung damit war auch der Brutansatz der in Flugzelten aufgestellten Völker mit Hasel- oder Erlenpollen nicht besser als mit den bisher geprüften Ersatzmitteln. Auch hier wird es notwendig sein —entsprechend den oben erwähnten Lebensdauerversuchen—, an Stelle der bisher meist verwandten Pollengemische verschiedener Zusammensetzung einzelne Pollenarten untereinander und mit den Ersatzmitteln zu vergleichen. Die zunächst auch für den Brutansatz vermuteten Wirkungsunterschiede zwischen handgesammeltem und gehöseltem Pollen gleicher Art bedürfen weiterer Prüfung. Vor allem bleibt zu untersuchen, ob derartige Unterschiede auch zwischen unverarbeiteten und von den Bienen eingetragenen Ersatzmitteln bestehen—eine Frage, welche für die Anwendung der Ersatzmittel in der Praxis von grösster Bedeutung ist. Im Spätsommer 1953 durchgeführte Vorversuche lassen Schlüsse noch nicht zu.

In besonderen Serien wurde versucht, die Wirkung der Pollenersatzmittel auf die Ausbildung der Pharynxdrüsen und den Bruteffekt experimentell zu trennen. Es ergab sich, dass für die Stärke des Brutansatzes nicht die Qualität des Futters ausschlaggebend ist, welches in den ersten Lebenstagen der Arbeitsbiene die Pharynxdrüsen zur Entwicklung bringt, sondern das während der Bruttätigkeit selbst zur Verfügung stehende Futter: Bienen, welche bis zur Entwicklung der Drüsen mit einem Ersatzmittel ernährt wurden, brüteten bei anschliessender Fütterung mit einem überlegenen Pollengemisch im Mittel aller Versuche ebenso gut wie durchgehend mit Pollen gefütterte Vergleichsbienen. Wurden umgekehrt Völkchen bis zur Entwicklung der Pharynxdrüsen unterschiedslos mit einem Pollengemisch, während des Brütens teils mit Ersatzmitteln, teils mit diesem Pollengemisch gefüttert, so war der Brutansatz der Völkchen mit Ersatzmitteln geringer als der mit Pollen brütenden Völkchen. Kontrollen zeigten, dass der Futterwechsel an sich ohne Bedeutung war. Ungeklärt ist dabei noch, ob der schlechtere Brutansatz auf eine geringere Futtersaftproduktion oder auf einen geringeren Nährwert der Ersatzmittel für die älteren Larven zurückzuführen ist, die bekanntlich nicht mit reinem Futtersaft sondern mit einem Mischfutter unter Zusatz von Honig und Pollen, bzw. Ersatzmitteln gefüttert werden. Jedenfalls mahnt dieses Ergebnis zur Vorsicht bei der Beurteilung von Pollenersatzmitteln nach der Ausbildung der Pharynxdrüsen.

Für die Gewinnung von gehöselten Ersatzmitteln mit Hilfe von Pollenfallen nach BÖTTCHER (1941, 1943) wurden Bienenvölker zum Abschluss von der natürlichen Tracht in der Winterhalle des Botanischen Gartens Marburg aufgestellt. Hierbei bot sich Gelegenheit, die Annahme von Blütenstaub und Ersatzmitteln unter gleichen Bedingungen an künstlichen Höselplätzen zu prüfen. Die Versuche zeigten, dass die Bienen bei freier Wahl Blütenstaub, auch den in der Wirkung den Ersatzmitteln nicht

überlegenen Hasel- und Erlenpollen, den Ersatzmitteln auch dann vorziehen, wenn diese mit einem Duftstoff angereichert wurden und die Bienen bereits tagelang auf sie eingeflogen waren. Dies bestätigt die alljährliche Beobachtung auf unserem Anstaltsbienenstand und die Erfahrung vieler Imker, dass Bienenvölker die Annahme von Pollenersatzmitteln an Höselplätzen und im Stock verweigern, sobald ihnen Pollen in ausreichender Menge zur Verfügung steht.

Die Untersuchung der Überwinterungsfähigkeit von Bienen, die ihren Winter-Eiweißfettkörper nur mit Ersatzmitteln bilden konnten, steht noch in den Anfängen. Sie stößt auf erhebliche Schwierigkeiten, weil bei Aufstellung der Völker im Freien das Eintragen von Blütenstaub auch mit Pollenfallen nicht völlig verhindert werden kann, die Völker aber, wenn man sie längere Zeit in Flugzelten hält, stark noseimakrank werden.

Weiter fortgeschritten ist dagegen die vergleichende Prüfung der Lebensdauer und Brutfähigkeit von Bienen, die mit Ersatzmitteln erbrütet wurden. Zur Feststellung der Lebensdauer werden Jungbienen, die bei den oben geschilderten Brutversuchen anfallen, gekäfigt und bei reiner Zuckerkost im Thermostat gehalten. Bei allen bisherigen Versuchen war die mittlere Lebensdauer der mit Pollengemischen erbrüteten Bienen unter diesen Bedingungen höher als der mit Ersatzmitteln erbrüteten Bienen. Die Unterschiede sind statistisch gesichert. Entsprechend den Ergebnissen bei den übrigen Testen war diese Überlegenheit nicht festzustellen bei Bienen, die mit handgesammeltem Haselpollen erbrütet wurden. Dagegen zeigten sich Unterschiede beim Vergleich von Pollenersatzmitteln mit verschiedener Brutwirkung, z.B. lebten die mit Bierhefe erbrüteten Bienen im Mittel der bisherigen Versuche länger als die mit anderen Ersatzmitteln erbrüteten Bienen. Da der Eiweißverbrauch gekäfigter Bienen nach LOTMAR (1939) sehr hoch ist und die Lebensdauer nach MAURIZIO (1950) entscheidend von den Eiweißdepots im Körper der Biene abhängt, darf die Lebensdauer frisch geschlüpfter Bienen bei eiweißfreier Kost wohl als ein Maß für die in der Larvenzeit angelegten Eiweißvorräte angesehen werden. Die Lebensdauer mit Pollenersatzmitteln erbrüteter Jungbienen bei reiner Zuckernahrung stellt damit einen weiteren wertvollen Test für den Nährwert der Ersatzmittel dar.

Die höchste Lebensdauer wiesen in diesen Versuchen Bienen auf, die aus Standvölkern oder im Freien (nicht in Flugzelten) gehaltenen Einwabenvölkchen stammten. Neben der Qualität des Larvenfutters scheinen also auch Stärke und Lebensbedingungen der Brutvölker eine Rolle zu spielen. Für die Anwendung von Pollenersatzmitteln in der Praxis ist ferner von Bedeutung, dass die festgestellten Unterschiede in der Lebensdauer verschwinden, wenn die frisch geschlüpften Bienen Eiweißfutter erhalten. Es ist daher nicht zu befürchten, dass mit Ersatzmitteln erbrütete Bienen unter natürlichen Bedingungen im Volk kurzlebig sind.

Versuche über die weitere Brutfähigkeit von Bienen, die mit Ersatzmitteln erbrütet wurden, habe ich bisher vorwiegend mit kleinen, im Thermostat gehaltenen beweiselten Völkchen durchgeführt. Sie gehen

bei Fütterung mit Pollen ohne Weiteres in Brut. Ein wesentlicher Unterschied zu Völkchen, die mit normal, d.h. mit Pollen erbrüteten Bienen gebildet wurden, scheint nicht zu bestehen. Wenn auch vergleichende Versuche mit stärkeren Völkern in Flugzelten oder im Freien noch fehlen, so kann aus diesen vorläufigen Ergebnissen immerhin geschlossen werden, dass die mit Ersatzmitteln erbrüteten Arbeitsbienen weiterhin brutfähig sind. Das Gleiche konnte ich auch für Königinnen nachweisen, die ich dadurch erhielt, dass ich mit Ersatzmitteln gefütterte Völkchen in Flugzelten entweiselte. Sie schaffen jederzeit Königinnen nach. Sogar im Brutschrank gehaltene Modellvölkchen aus wenigen hundert Bienen können durch Entweiseln veranlasst werden, Königinnen nachzuziehen, auch wenn sie vorher im weiselrichtigen Zustand keine Arbeiterinnenbrut bis zum Verdeckeln brachten. Hierbei zeigten sich charakteristische Unterschiede zwischen den mit Pollengemischen oder Ersatzmitteln ernährten Völkchen, die noch weiter verfolgt werden sollen. Ein Teil der so erhaltenen Königinnen wurde fixiert und ist noch auf die Ausbildung der „königlichen“ Merkmale und Organe, vor allem auf die Zahl der angelegten Eischläuche zu untersuchen. Bisher 6 Königinnen wurden nach erfolgter Begattung in Versuchsvölkchen oder Standvölker eingeweiselt. In ihrer Legeleistung zeigten sie bisher keine feststellbaren Unterschiede zu anderen, mit Pollen erbrüteten Nachschaffungsköniginnen und scheinen damit vollwertig zu sein.

Abschliessend lässt sich sagen, dass Bierhefe, Torula-Hefe (Höselhefe) und Vollsojamehle als brauchbare Pollenersatzmittel anzusehen sind. Mit Kohlenwasserstoffen entfettetes, sog. Bäckersojamehl ist dagegen fast ohne Nährwert für die Biene und als Pollenersatz ungeeignet. Keines der bisher geprüften Ersatzmittel erreicht die Wirkung hochwertiger Pollenarten, zumindest nicht die Wirkung natürlicher Pollengemische, wie sie den Bienenvölkern bei Pollentracht oder in einer vom Imker zugegebenen Pollenwabe zur Verfügung stehen. Die Ersatzmittel sind jedoch geringerwertigen Pollenarten wie Hasel- und Erlenpollen mindestens ebenbürtig und Koniferenpollen offenbar wesentlich überlegen. Mit Ersatzmitteln erbrütete Arbeitsbienen und Königinnen scheinen vollwertige Bienenwesen zu sein. Bei gleichzeitigem Angebot ziehen die Bienen Pollen jedem Ersatzmittel vor. Dies mindert aber den Wert der Ersatzmittel für die imkerliche Praxis ebenso wenig wie ihre Unterlegenheit gegenüber hochwertigen Pollenarten und Pollengemischen; denn sie sollen den Blütenstaub nicht in jedem Falle ersetzen sondern lediglich Lücken in der natürlichen Pollenversorgung der Bienenvölker schliessen.

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CORRESPONDANCE

Nous avons reçu de M. le professeur T. C. SCHNEIRLA la lettre suivante :

In number 1 of volume 1, 1954, this journal, p. 7-19, Dr. Karlheinz BIER has an interesting article under the title *Ueber den Einfluss der Königin auf die arbeiterinnen Fertilität im Ameisenstaat*, a significant contribution to the reproductive biology of the social insect colony. In one connection (p. 15), he has occasion to refer to my investigations on the *Eciton* behavior pattern, as follows:

„Den eindruckvollsten Beleg für die gegenseitige Bedingtheit von Brut und Fertilität bilden die von SCHNEIRLA erforschten Verhältnisse bei den *Eciton*-Arten. So lange Larven vorhanden sind produziert die ♀ keine Eier. Erst nachdem sich alle Larven verpuppt haben, wird die ♀ ausgeprägt physogastrisch und legt dann innerhalb weniger Tage über 20 000 Eier ab. Die Larven schlüpfen bald und die Eiablage ruht nun bis zur Verpuppung der heranwachsenden Brut. Wenn auch SCHNEIRLA (1944) den Grund für diesen Zyklus nur in der Verhaltensweise der Königin sieht, so darf dabei die ernährungsphysiologische Seite der Vorgänge nicht übersehen werden; denn es ist einleuchtend, dass sich nur eine Verhaltensweise herausbilden kann, die in Uebereinstimmung mit den physiologischen Gegebenheiten steht.”

Herr Dr. BIER refers only to a paper I published in 1944 (1) concerned specifically with the queen's rhythmic function. Unfortunately, this paper presented only a part of my results on that problem, preliminary to more conclusive evidence which I have published subsequently. But his statement that I have overlooked the nutritive-physiological aspects of the process is not correct even for the 1944 paper taken alone.

First, I should like to call attention to what I actually said in the 1944 publication. On page 176, following a diagrammatic representation and the italicized heading *Theoretical Explanation of the parallelism between brood condition and colony behavior*, appears the statement:

“These facts suggest that a causal relationship exists between the condition of the brood and the circumstances of general activity in the colony...” “This idea has been advanced in a previous connection...” (2). Evidence is then summarized concerning stimulative relationships between broods and workers both in nutritive and general activities. From such stimulation “an *Eciton* worker population receives

(1) 1944. *Jour. N. Y. Entom. Soc.*, vol. 52, p. 153-192.

(2) 1938. *Jour. Comparative Psychol.*, vol. 25, p. 51-90.

a great lift in internal 'drive'... (p. 179)." "Our theory thus accounts for the nomadic-statory cycle of *Eciton* colony activity in terms of cyclical changes in the internal stimulative properties of different broods" (p. 180). This theory is featured in the summary (p. 190) as follows: "The intimate correspondence which exists between colony behavior and brood condition is explicable in terms of the WHEELER *trophallaxis* concept. Evidence is cited for the involvement of a special social-stimulative effect, a super-added 'drive' factor furnished by broods..." at specified critical times.

As concerns the queen, her functions, "... serve indirectly as a pace-making factor in the colony behavior pattern..." (p. 189). "By furnishing new broods at fixed intervals, the queen's function indirectly governs the presence or absence of the intra-colony dynamizing factor critically responsible for the ebb and flow of events in the *Eciton* behavior pattern" (p. 191).

The next problem, of course, was to investigate the relationship between the queen's rhythm and the colony functional pattern. This question I have studied during the past ten years in relation to other causal factors in the cycle. The results have been reported in a series of papers, particularly: 3, pp. 66-67; 4, see especially pp. 344-345; 5, see pp. 23ff.; 6, pp. 253-257; and 7, see pp. 30-33. In these publications I have developed the view that the queen's rhythm is controlled not endogenously, but through an extrinsic interrelationship grounded in the brood-colony trophallactic process described in 1938 (2). Here is an explicit statement:

"The pacemaker function seems not to be endogenous to the queen, and dependent upon some internal rhythm... Instead we find that each new egg-laying episode is set off by an intrinsic change arising at a particular juncture in normal colony functions (7, p. 31)... These occurrences, regularly associated with the termination of a nomadic phase, are adequate to prepare the queen for a massive egg-laying operation..." (7, p. 32). "My theory therefore is that the queen is set off into each new egg-production episode in a 'feed-back' fashion, by events in the activity cycle which themselves are indirect results of the queen's own function at an earlier point in the cycle" (7, p. 32).

Thus, since the initial stages of investigation (8) I have recognized the significance for *Eciton* colony function of prevailing physiological circumstances in the colony. The theory offered at an early stage of the work (2, 9) has served throughout to emphasize the importance of physiological processes in the causal basis of the pattern, in the biological and behavioral interrelationships of worker population, queen, and brood.

T. C. SCHNEIRLA.

(3) 1949. *Bulletin Amer. Museum Nat. History*, vol. 94, p. 1-82.

(4) SCHNEIRLA (T. C.), BROWN (R. Z.), 1950. *Ibid.*, vol. 95, p. 263-353.

(5) SCHNEIRLA (T. C.), BROWN (R. Z.), 1952. *Zoologica*, vol. 37, p. 5-32.

(6) 1952. *Coll. internat. C. N. R. S.*, Paris, vol. 34 p. 247-269.

(7) 1953. *Bull. Union inter. Étude Ins. Soc.*, t. 1, n° 3, p. 29-41.

(8) 1933. *Jour. Comparative Psychol.*, vol. 15, p. 267-299.

(9) 1945. *Biol. Bulletin*, vol. 88, p. 166-193.

NOUVELLES ESPÈCES DE TERMITES DÉCRITES AU COURS DES ANNÉES 1952 ET 1953

1952. SNYDER (T. E.). — A New *Rugitermes* from Guatemala (*Proc. Ent. Soc.*, Washington, **54** (6), 303-305).
1952. EMERSON (A. E.). — The neotropical Genera *Procornitermes* and *Cornitermes* (*Isoptera : Termitidæ*) (*Bul. Amer. Mus. Nat. Hist.*, **99**, 475-540).
1953. EMERSON (A. E.). — The African genus *Apicotermes* (*Isoptera : Termitidæ*) (*Ann. Mus. Royal Congo Belge, Sc. Zool.*, **17**, 99-121).
1953. HARRIS (W. V.). — A new Termite from the Belgian Congo (*Rev. Zool. Bot. Afr.* **47** (3-4), 261-262).
1953. AHMAD (M.). — New Termites and a hitherto unknown Caste Ceylon (*Spolia Zeylanica*, **27** (1), 37-41).
1953. ROONWAL (M. L.). — Systematics of Oriental Termites : n° 1. A new Species of Termites, *Heterotermes gertrudæ*, s. nov., from North India (*Isoptera*, Family *Rhinotermitidæ*) (*India Jour. Ent.*, **15** (2), 115-118).

The new species described in these publications were:

- Rugitermes unicolor* Snyder 1952. Imago, soldier. Guatemala.
- Procornitermes araujo* Emerson 1952. Imago, soldier. Brazil.
- Procornitermes romani* Emerson 1952. Soldier. Brazil.
- Cornitermes snyderi* Emerson 1952. Imago, soldier. Bolivia. Brazil.
- Cornitermes falcatus* Emerson 1952. Soldier. Brazil.
- Cornitermes weberi* Emerson 1952. Soldier. British Guiana.
- Cornitermes incisus* Emerson 1952. Soldier. Brazil.
- Cornitermes villosus* Emerson 1952. Soldier. Brazil.
- Cornitermes ovatus* Emerson 1952. Soldier. Brazil.
- Cornitermes bequaerti* Emerson 1952. Soldier. Brazil.
- Apicotermes desneuxi* Emerson 1953. Imago, soldier. Belgian Congo.
- Apicotermes porifex* Emerson 1953. Soldier. Belgian Congo.
- Microtermes pallidiventris* Harris 1953. Imago. Belgian Congo.
- Coptotermes emersoni* Ahmad 1953. Soldier. Ceylon.
- Odontotermes (Hypotermes) winifred* Ahmad 1953. Imago, soldier. Ceylon.
- Heterotermes gertrudæ* Roonwal 1953. Soldier, worker. India.

II

NOUVELLES DE L'UNION

LA VIE DES SECTIONS

SECOND ANNUAL MEETING OF NORTH AMERICAN SECTION IN LOS ANGELES, CALIFORNIA, DEC. 27, 1953

The second annual meeting of the American Section of the International Union for the Study of Social Insects was held in conjunction with the meeting of the Entomological Society of America in Los Angeles, California, on December 7, 1953. In the absence of the chairman and secretary, Dr. Charles D. MICHENER served as chairman pro tem. A symposium was held on ecological methods for the study of social insects. Dr. Orlando PARK of Northwestern University spoke on myrmecophilous pselaphid beetles; Dr. Frances WEESNER of the University of California spoke on the ecology of southwestern American termites; Dr. Joseph F. REINHARDT of Huron, California, spoke on the responses of bees visiting the flowers of alfalfa, and Dr. Edward S. Ross of the California Academy of Sciences spoke on the use of photography in the study of social insects.

TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

1944. BISGAARD (CH.). — **Meddelelse om nogle nye Myrer for Danmarks Fauna** (With an English summary) (*Entomol. Meddel.*, vol. **25**, p. 115-126, 2 fig.).

I. The first time *Formica uralensis* Ruzsky was found here in Denmark was in Jutland in the summer of 1938. Only one little nest was situated on the borderland of a moor and although the nest was not disturbed, this species is first found again at this moor in July 1953. This time it lived together with *Formica picea*, who is known as one of the host-species of *F. uralensis*.

During the above-mentioned 15 years a few nests of *F. uralensis* were seen on a neighbouring moor.

II. The entrance holes to several nests of *Myrmica schencki* Emery found in 1939 were provided with a tubular prolongation, which was constructed by plant fragments joined together.

It appeared that Dr. Stärcke (*Tijdsch. v. Ent.*, **70**, p. 41, 1927, and **71**, p. 44, 1928) had already described these peculiar entrances calling them "chimneys".

III. A queen of *Anergates atratulus* Schenck was found on the island of Bornholm in a colony of about a hundred *Tetramorium* workers together with some worker-pupæ and some nearly full-grown larvæ.

In papers dealing with *Anergates* it is emphasized, however, that *Tetramorium*-brood is never found in colonies of *Anergates*. In this case the gaster of the queen was only a little swollen, and it seems that the adoption has taken place recently, and that the brood of the former *Tetramorium* queen has not yet hatched.

1948. BOETIUS (J.). — **Sortfarvningssygdom i danske Bigaarde 1944-1947** (*Maanedsskrift for Dyrlaeger*, vol. **59**, p. 413-23).

A status of bee paralysis in Danish apiaries is given for the years 1944-1947. Bee paralysis forms a complex of diseases, the greater part of the Danish cases most likely belonging to an infectious type. Transmission seems to take place by drifting and not by exchange of combs.

1948. BOETIUS (J.). — **Ueber den Verlauf der Nektarabsonderung einiger Blütenpflanzen** (*Beih. z. Schweizerischen Bienenzeitung*, vol. **2** (Heft **17**), p. 257-317).

Die Arbeit behandelt Untersuchungen über Trockensubstanzgehalt in Blütenpflanzen in Beziehung zu Entwicklungsstufen der Blüten. Zudem werden die vom BEUTLER und KLEBER nachgewiesenen täglichen Rhythmen in der Sekretion näher analysiert. Weiter ist der Einfluss durch Bienenbesuch und Witterung auf der Sekretion untersucht. Schliesslich wird eine tabellarische Uebersicht über die Nektarproduktion von 41 untersuchten Blütenpflanzen gegeben.

1947. CONSANI (M.). — Reperti corologici sulle formiche itamiane (*Redia*, **32**, 179-182). — 1947. Primo contributo alla conoscenza della fauna entomologica del Matese. Imenotteri (*Formicidæ*) (*Boll. Assoc. Romana Entom.*, **2**, 28-29). — 1948. Interessante reperto su *Embolemus ruddii* Westkood (*Hymenoptera, Bethyloidea, Embolemidæ*) (*Redia*, **33**, 123-125, 1 fig.). — 1949. Formiche raccolte nell'Appenninico Abruzzese dal Sig. Pio Bisleti (*Boll. Assoc. Romana Entom.*, **4**, 11-12). — 1950-1951. Formiche dell'Africa Orientale (*Boll. Ist. Entom. Univ. Bologna*, **18**, 167-172, 4 fig.). — 1951. Formiche di Puglia e delle Isole Tremiti (*Mem. Biogeogr. Adriatica*, **2**, 25-31). — 1951, e MENOZZI (C.). Missione biologica Sagan-Omo diretta dal Prof. E.

- Zavattari. *Hymenoptera, Formicidae* (*Riv. Biol. Coloniale*, **11**, 57-71, 4 fig.). — 1952. e ZANGHERI (P.). Fauna di Romagna. Imenotteri-Formicidi (*Mem. Soc. Entom. Ital.*, **31**, 38-48). — 1952. Un caso di omonimia nel genere *Crematogaster* (*Hymenoptera, Formicidae*) (*Boll. Soc. Entom. Ital.*, **82**, 100).
1937. GHIDINI (G. M.). — Su alcuni *Termitidi* di Sumatra raccolti da E. Jacobson (*Atti Soc. It. Sc. Nat.*, **76**, 317-329). — 1937. I Reali di terza forma in *Reticulitermes lucifugus* Rossi (*Mem. Soc. Ent. It.*, **16**, 25-36). — 1937. Ulteriori risultati negli allevamenti di *Reticulitermes lucifugus* Rossi (*Boll. Soc. It. Biol. Sper.*, **12**, 633-634). — 1937. Missione del Prof. E. Zavattari nel Paese dei Borana-Nuove specie di *Termitidi* (*Boll. Soc. Ent. It.*, **62**, 141-143). — 1938. Ninfe soldati in *Reticulitermes lucifugus* Rossi ottenute in allevamento (*Arch. Zool. It.*, **25**, 95-107). — 1938. La presumibile funzione delle spugne legnose nei nidi dei *Metatermitidi* (*Riv. Biol. Colon.*, **1**, 261-267). — 1939. Le spirochete presenti in *Reticulitermes lucifugus* Rossi (*Riv. Biol. Colon.*, **2**, 125-140) (in collab. con I. ARCHETTI). — 1939. Sulla presenza di acetilcolina in *Reticulitermes lucifugus* e *Calotermes flavicollis* (*Riv. Biol. Colon.*, **2**, 207-213). — 1939. Sulle concrezioni pericardiali nelle termiti (*Riv. Biol. Colon.*, **2**, 345-353) (in collab. con M. MORIGGI). — 1939. Ricerche sul quoziente respiratorio nelle diverse caste di *Reticulitermes lucifugus* Rossi (*Riv. Biol. Colon.*, **2**, 385-399). — 1940. Ricerche sulla attività cellulolitica della flora e della fauna intestinale di *Reticulitermes lucifugus* Rossi (*Boll. Soc. It. Biol. Sper.*, **15**, 220-221). — 1941. A proposito di alcune recenti ricerche sulla cellulolisi nell'intestino delle termiti (*Boll. di Zool.*, **12**, 103-113). — 1941. Le gregarie delle termiti con descrizione di una nuova specie *Riv. Parassit.*, **5**, 161-175) (in collab. con M. MORIGGI). — 1942. *Trichonympha scortecci* nuova specie di Flagellato vivente in *Psammodermes hybostoma* Desn. (*Boll. di Zool.*, **13**, 5 p.). — 1942. Le *Trichonympha* di *Reticulitermes lucifugus* Rossi (*Riv. Biol. Colon.*, **5**, 19-40). — 1942. Regressione delle gonadi ed evoluzione delle caste sterili nelle termiti (*Arch. It. Anat. e Embriol.*, **47**, 825-831) (in coll. con E. STELLA). — 1946. Il *Reticulitermes lucifugus* può attaccare piante viventi (*Boll. Soc. Ent. Ital.*, **76**, 42-46) (in coll. con F. CAPRA). — 1949. Ricerche biologiche su *Iridomyrmex pruinosus humilis* Mayr. (*Boll. Soc. Entom. It.*, **72**, 58-62). — 1952. L'Ape (*La Scuola-Brescia*, 1-73).
1920. JUCCI (C.). — Sulla differenziazione delle caste nelle società dei Termitidi. N. 1 e 2 (*Rendic. Accd. Lincei*, vol. **29**, ser. 5^o, 2^o sem., fasc. 1^o-2^o, p. 69-71, 95-98). — 1921. Sulla presenza di depositi uratici nel tessuto adiposo dei Termitidi (*Rend. Acc. Lincei*, vol. **30**, ser. 5^o, 1^o sem., fasc. 3^o, p. 92-95). — 1921. Sul metabolismo dei reali veri nella società dei Termitidi (*Rend. Acc. Lincei*, vol. **30**, ser. 5^o, 1^o sem., fasc. 7^o, p. 213-15). — 1924. Su la differenziazione delle caste nella società dei Termitidi. I Neotenici (Reali veri e neotenici. L'escrezione nei reali neotenici. La fisiologia della biologia) (*Memorie Acc. Lincei*, **14**, **9**, p. 267-500, 21 fig., 4 tav.). — 1926. Le cellule nutrici degli spermi nel re delle Termiti (*Boll. Soc. It. Biol. sperim.*, **1**, **3**, p. 248-50). — 1926. Il problema delle caste nei Termiti (*Revista di Biologia*, **7**, **3**, p. 404-409). — 1930. La biologia sessuale nelle Società degli insetti e le cellule nutrici degli spermi (*Proceed. 2^o Intern. Congr. f. sex. research*, Edinburgh, p. 231-238). — 1931. Sulla presenza di batteriociti nel tessuto adiposo dei Termitidi (*Arch. Zool. It. Vol. Atti XI Congr. Intern. Zool. Padova*, **3**, p. 1422-1428). — 1936. L'allevamento del *Reticulitermes lucifugus* in tubi da saggio (*Rend. R. Accad. Nazion. d. Lincei*, vol. **29**, **9**). — 1937. Allevamenti di *Reticulitermes lucifugus* in provetta (*Boll. Soc. Ital. di Biol. Sperim.*, **12**, **1**). — 1937. Le Termiti nelle nostre Colonie Africane (*Atti Soc. Ital. Progresso Scienze, XXV Riunione Tripoli*, 1936). — 1938. Il problema delle Termiti nell'Africa Orientale Itamiana (*Rivista di Biologia*, **25**). — 1953. Simbiosi e filogenesi negli insetti (*Trans. Ninth Int. Congr. Ent.*, **1**).
1930. JUCCI (C.) e BUYA (B. M.). — Sul tessuto adiposo del *Termopsis angusticollis* (*Studi Sassaesi*, **14**).
1953. JUCCI (C.), SPRINGHETTI (A.). — Evolution of seminal vesicles in Isoptera (*Trans. Ninth Int. Congr. Ent.*, **1**). — 1953. Contributo allo studio delle Termiti in

Italia per l'impostazione razionale della lotta antitermica I Esplorazione in Sicilia (*Est. dal « Bol. Ist. Pat. Libro »*).

1948. GUIGLIA (D.). — Le vespe d'Italia (*Mem. Soc. Entom. It.*, **27**, 1-83).

1952. SPRINGHETTI (A.). — Le vescicole seminali in *Mastotermes* e in *Macrotermes* (*Rend. Ist. Lombardo*, **85**). — 1953. Le vescicole seminali in *Zootermopsis* e in *Blattella* (*Ist. Lomb. Scien. Sett. Hoepli*).

1952. VENTURI (F.). — Notule Dipterologiche : revisione sistematica del genere *Metopia* Meigen in Italia (*Boll. Entom. Un. Bologna*, **19**).

1943. LARSSON (SV. G.). — **Myrer, Danmarks Fauna**. Vol. **49**, p. 1-190, 99 fig.

The publication enters as a part of the serie « Danmarks Fauna » and appears in Danish; it is in the main compilatory and contains the following sections: a general morphological and biological summary (45 p.), a systematical summary of the Danish ant-fauna (115 p.), a list of antguests (25 p.) and a very brief bibliography. Outside Scandinavia the book is of great importance as a fauna-list (numbered genera and species).

1943. LARSSON (SV. G.). — **Myrerne som Bymestre** (*Dyr i Natur og Museum*, 1942-1943, p. 37-53, 14 fig.).

Mainly a referring description of nest-building by the ants, especially under Danish circumstances.

1947. LARSSON (SV. G.). — **Havemyrens forunderlige Liv** (*Mærkelige Dyr*, København, p. 28-47, 13 fig.).

Mainly a referring description of the biology of *Lasius niger* and *Lasius flavus*. Among the original figures may be emphasized a sketch of a *Lasius flavus*-nest, where a passage from the winter-nest is leading almost vertically through a layer of clay (90 cm) to a narrow water containing layer of gravel, where it expands into a little room.

1938. STELLA (E.). — **Ricerche Citologiche sui neutri e sui riproduttori delle Termiti Italiane** (*Calotermes flavicollis* e *Reticulitermes lucifugus*) (*R. Acad. Naz. Lincei*, **7**, 1-30). — 1939. **Studi sulle Termiti, Comportamento citologico delle gonadi in operai di *Reticulitermes lucifugus* R.** (*Riv. Biol. Col.* **2**, 81-95). — 1939. **Studi sulle Termiti, Alcuni dati citologici sulle gonadi di soldati di *Bellicositermes bellicosus*** (Smeath) (*Riv. Biol. Col.*, **2**, 255-262).

1942. STELLA (E.) e GHIDINI (G. M.). — **Regressione delle gonadi ed evoluzione delle caste sterili nelle Termiti** (*Arch. It. di Anat. ed Embr.*, **47**, 825-831).

1936. IWATA (K.). — **On the habits of *Stizus* and *Bembix* which occur in Japan** [*Kontyu*, **10**, 233 (in Japanese)].

Observations on the habits of *Stizus japonicus*, *S. formosanus* and *Bembix niponica*

1938. IWATA (K.). — **Habits of some bees in Formosa** [(II-IV), *Tr. Nat. Hist. Soc. Formosa*, **28**, 205, 257, 372 (in Japanese)].

Observations on the habits of 3 genera of bees forming a chain of gradual development in sociality, *Xylocopa*, *Ceratina* and *Allodape*. A peculiarity of the last mentioned genus, the common nest cavity without separated cells (Brauns) was confirmed in *Allodape marginata* Sm.

1940. IWATA (K.). — **Decline of wasps and bees' communities** [*Akitsu*, **2**, 170 (in Japanese)].

The communities of solitary but gregarious wasps and bees can increase at first their size, esp. by artificial supply of nest-material. But the reproductive rate of

their parasites is usually much higher than that of the hosts, consequently the communities are in due time destroyed and finally abandoned. Because of the lack of communal defense as found in social Insects, the maintenance of the species-life depends mostly on the migration of certain pioneers from the original communities into other niches.

1942. IWATA (K.). — **Comparative studies on the habits of solitary wasps** (*Tenthredo*, 4, nos. 1-2, 146 p.).

Comparative considerations of habit-types of all the hunting-wasps with respect to the following points: oviposition, kind of prey, operation and transportation of prey, provisionment, nidification, closing and opening of nest entrance. Correlations betw. component-habit system and habit-type system were discussed. Colonization and subsociality were also briefly referred.

1950. IWATA (K.). — **Hypothetic habit-type trees of the aculeate Hymenoptera** [*Techn. Bull. Kagawa Agr. College*, 1, 75 (in Japanese with English résumé)].

Basing upon the treatise in 1942 and some additional knowledges, the habit-formulae for each group of Aculeata were described and shown as habit-type trees.

1951. IWATA (K.), MORIMOTO (R.), YASUMATSU (K.). — See MORIMOTO.

1939. MORISITA (M.). — **On the daily rhythm of activity of ants. I, Activity of *Formica fusca* var. *japonica* Motschulsky** [*Ecol. Rev.*, 5, 105 (in Jap. with English résumé)].

Food-hunting begins in early spring, ends in late autumn and ceases in any season at night in Kyoto. In spring and autumn, activity begins after sunrise and ceases before sunset, while in summer, begins a little before sunrise and ceases a little after sunset. These seasonal differences of activity seem to be caused by the effect of temperature and light. The cessation in summer night is caused by the decrease of light (below ca. 5 lux) and that in spring or autumn by the low temperature of air or soil surface (below 14°-15° C.).

1939. MORISITA (M.). — **On the daily rhythm of activity of ants. II, Activity of *Lasius niger* L.** [*Ecol. Rev.*, 5, 171 (in Jap. with English résumé)].

L. niger is active from early spring to late autumn in Kyoto with the following seasonal differences: In early spring, active only in daytime; in mid-late spring, active also at night though with a less degree; in summer more active at night than in daytime; in autumn natural activity decreases again. Preference of night to daytime can be supposed. Cessation or decrease of the nocturnal activity in spring or autumn seems to be caused by the low temperature, the increase of activity in summer night is caused probably by the high temperature.

1939. MORISITA (M.). — **On the battles between *Tetramorium caespitum* ssp. *jacoti* Wheeler and other species of ants** [*Tr. Kansai Entom. Soc.*, 8 (in Jap. with English résumé)].

Battles betw. *Tetramorium* and *Lasius niger* or *Pristomyrmex pungens* are caused by the attacks of the first sp. After the victory, often *Tetramorium* occupies nests and trees producing honey dew which had been utilized previously by *Lasius*. The battles occur only in summer and are seemingly made to enlarge the territory and to secure the sufficient food supply for the increase of nest members.

1939. MORISITA (M.). — **The interrelations of several species of ants on a tree** [*Tr. Kansai Entom. Soc.*, 9, Pt. 2 (in Japanese)].

Interrelations among *Formica fusca* var. *japonica*, *Lasius niger*, *Crematogaster sordidula* ssp. *osakensis*, *Pristomyrmex pungens* on *Carpinus laxiflora* and *Betula ulmifolia* (excl. *Crematogaster*). Behavioral pattern of these ants can be divided into 2 types:

Lasius-and *Formica*-type. 3 spp. belonging to the former type climb up the tree in a procession, occupy the definite branches and attack the intruders. *Formica* forages individually from the branches occupied by *Lasius*-type spp. in the sly of occupants. No attacks of *Formica* to the occupants are observed. Among 3 *Lasius*-type spp., the balance of power varies from day to day. On a *Carpinus*, the former dominant, *Crematogaster*, was driven away by *Lasius*. Equilibrium betw. *L.* and *P.* differs in daytime ant at night. At night *P.* is completely driven away by *L.* probably due to the increase activity of *L.*, but *P.* intrudes again into the *L.*-branches in the next morning.

1941. MORISITA (M.). — **On *Camponotus herculeanus* ssp. *vagus* var. *yessensis* [Teranishi, *Mushi*, 13, 93 (in Japanese)].**

Notes on the distribution.

1941. MORISITA (M.). — **An application of the quadrat method to the estimation of the population density of moving animals (1) [Ecol. Rev., 7, 63 (in Jap. with English résumé)].**

Theoretical considerations show that, when a quadrat is prepared in an area, the relation among the mean indiv.-number of an animal sp. in the quadrat (d), mean number of the animals invading into the quadrat per unit time (s) and the mean time for which the animals stay in the quadrat (t) can be represented by $d = st$. The fitness of this formula to the population of *Formica fusca japonica* has been tested in various ways. The results indicate that the formula is good enough to be applied to the pop. of the ant observed and may probably be used for the study of other moving animals.

1945. MORISITA (M.). — **Ants [in H. Furukawa's "Insects", vol. 2, 1-56, Tokyo (in Japanese)].**

A general contribution of ants with the following contents: position of ants in nature and their life mode, species and distribution, habitat and nest, slavery ants. Descriptions are chiefly based upon the Japanese materials.

1945. MORISITA (M.). — **Ants of the southernmost district of Hokkaido [*Mushi*, 16, 21 (in Japanese)].**

List of 24 spp. from the district. Affinity of myrmecofauna betw. southern Hokkaido and northern Honshû was suggested.

1933. YASUMATSU (K.). — **On a new variety of *Psithyrus sylvestris* (Lepeltier) from Korea [Ins. World, 34, 41 (in Jap. with English résumé) var. *popovi* nov.].**

1934. YASUMATSU (K.). — **Eine neue, *Bombus ignitus* Smith ähnliche Schmarotzerhummel aus Korea (Hym., Bombidæ) [Ann. Zool. Jap., 14, 399, *Psithyrus* (*Ashtonips*) *coreanus* sp. nov.].**

1934. YASUMATSU (K.). — **On the male of *Bombus bicoloratus* Smith (Hym., Bombidæ) (Tr. Nat. Hist. Soc. Formosa, 34, 135).**

1934. YASUMATSU (K.). — **Les Hyménoptères de l'île Yakushima (*Mushi*, 7, 61).**

Notes sur distribution de quelques espèces de *Bombus* et *Vespidæ*.

1935. YASUMATSU (K.). — **Superfamily Apoidea, Insects of Jehol VIII, Order Hymenoptera, 2, 47 p. (Rep. First Sci. Exped. Manchukuo, 5, 1, 12, 167).**

Records of 7 spp. of *Bombus* including *B. (Lapidariob.) jeholensis* sp. nov.

1935. YASUMATSU (K.). — **Notes on two Apoidea collected by Prof. Tohru Uchida on the Mariana and West Caroline Islands (*Mushi*, 8, 94).**

Melipona (Trigona) atome Kll. from Palau Is.

1935. YASUMATSU (K.). — **Further notes on the hymenopterous fauna of the Yaeyama group (Ann. Zool. Jap., 15, 33).**

Records of *Ropalidia variegata*, *Vespa formosana* and *Polyrhachis dives* in Yonakuni Is, *Polistes yeyamensis* in Haderuma Is.

1937. YASUMATSU (K.). — *Lasius fuliginosus* (Latreille) var. *spathepus* Wheeler and its synechthrans, *Zyras comes* Sharp and *Zyras congnatus* Märkel var. *japonicus* Sharp [*Nippon no Kôtyû*, 1, 47 (in Jap.)].

List of *Zyras* spp. attacking *Lasius fuliginosus* and an observation on the behaviour of mentioned Staphylinids. These two spp. were found abundantly in a procession of the host ant. The injured ants were immediately attacked by them.

1937. YASUMATSU (K.). — **Hymenoptera of Tsushima (First Report), Fukuoka Hakubuts** [*Zasshi*, 2, 59 (in Japanese)].

Including notes on social Insects.

1938. YASUMATSU (K.). — **On the larva of *Allodape marginata* Sm.** [*Tr. Nat. Hist. Soc. of Formosa*, 28, 380 (in Japanese)].

Description of external characters.

1939. YASUMATSU (K.). — **On the occurrence of the Genus *Psithyrus* Lepeltier in Honshû, Japan (Hym., Bombidæ)** [*Konchû-Kenkyû*, 3, 18 (in Jap. with English résumé)].
Ps. (Fernaldaeps.) norvegicus japonicus spp. nov.

1939. YASUMATSU (K.). — **Notes on some species of the Genus *Psithyrus* Lepeltier from Korea (Hym., Bombidæ)** [*Tr. Kansai Entom. Soc.*, 9, Pt. 2 (in Japanese)].

Records of 4 spp. including *Ps. (Ps.) branickii doii* spp. nov.

1939. YASUMATSU (K.), BEQUAERT (J.). — **Vespoidea of Micronesia (Hym.)** (*Tenthredo* 2, 314).

Records of *Polistes olivaceus*, *P. semiflavus*, *Ropalidia marginata* v. *sundaica*.

1940. YASUMATSU (K.). — **Contribution to the hymenopterous fauna of Inner Mongolia and North China** (*Tr. Sapporo Nat. Hist. Soc.*, 17, 90).

Records of ants (2 spp.) and bumblebees (5 spp.) with *Bombus (Subterraneob.) chaharensis* sp. nov.

1940. YASUMATSU (K.). — **Hymenoptera collected in Tadao Kano's Expeditions to Botel-Tobago Island. IV, Vespidae, Larridae and Chrysididae** (*Tr. Sapporo Nat. Hist. Soc.*, 16, 96).

Records of *Vespa* (3 spp.) and *Polistes* (2 spp.).

1940. YASUMATSU (K.). — **Beitrage zur Kenntnis der Ameisenfauna Mikronesiens. I, Die Ameisengattung *Anochetus* Mayr der Karolinen** (*Ann. Zool. Jap.*, 19).

A. (A.) minutus Karawajew u. *A. (A.) splendidulus* sp. nov., mit biologischen Notizen von Prof. T. Esaki.

1940. YASUMATSU (K.). — **Matériaux pour servir à la faune myrmécologique des îles de Yaeyama** (*Mushi*, 13, 67). — 1940. Ants collected by Mr. H. Takahasi in Hingan (Hsingan) North Province, North Manchuria (Hym., Formicidae) [*Tr. Sapporo Nat. Hist. Soc.*, 31, 182 (in Japanese)].

1941. YASUMATSU (K.). — **On the ants of the genus *Dolichoderus* of Angaran element from the Far East (Hym., Formicidae)** [*Kontyû*, 14, 177 (in Japanese)].

D. quadripunctatus sibiricus Emery was recognized as a single representative of the genus in the Far East.

1945. YASUMATSU (K.). — **Vespoidea of Micronesia, II (Hym.)** (*Mushi*, 16, 35).

On *Ropalidia marginata sundaica*.

1946. YASUMATSU (K.). — **An observation of the soil fauna beneath the nest of *Vespa mandarina* Smith in a tree-hollowa : quantitative study of the macroscopic fauna** [*Matsumushi*, 1, 1 (in Japanese)].

Interspecific relationships of the inhabitants consisting of 37 spp. were analysed in connection with the food-chain among them. A remarkable biological richness of the environment examined was discussed.

1946. YASUMATSU (K.). — *Hymenoptera Aculeata* collected by Mr. K. Tsuneki in North China and Inner Mongolia. III, *Apoidea*, 1 (*Mushi*, 17, 19).

Records of 2 spp. of *Bombus*.

1947. YASUMATSU (K.). — Some wasps and bees of the desert Kunshan-Tagh in Inner Mongolia (*Mushi*, 18, 29).

Records of 2 spp. of *Bombus*.

1948. YASUMATSU (K.). — *Ants and human life* [XI + 199p., Tokyo (in Japanese)]. With an introductory by T. ESAKI.

A review on the relationships betw. ants and various aspects of human life.

1948. YASUMATSU (K.). — *Distribution of Ants* [*Kyôdo Shizenkagaku no Kenkyû*, 1, Mountain and Plateau, 185 (in Japanese)].

A review on the distribution of ants, including the following items : 1. Phylogeny ; 2. Mode of distribution ; 3. Geographical distr. ; 4. Vertical distr. ; 5. Ecological distr. ; 6. Population density.

1949. YASUMATSU (K.). — *Synonymy and other taxonomic notes on the two commonest bumble bees of eastern Asia* (*Ins. Mats.*, 17, 17).

B. (Pratob.) ignitus Smith and *B. (B.) speciosus* Smith were discussed.

1950. YASUMATSU (K.). — *Discovery of an ant of the genus Lordonyrma Emery in Eastern Asia (Hym.)* (*Ins. Mats.*, 17, 73).

Discussion of the genus, esp. on the distribution and description of *L. nobilis* sp. nov. from Japan.

1951. YASUMATSU (K.). — *Bombus and Psithyrus of Shansi, N. China* (*Mushi*, 22, 59).

3 spp. of *Psithyrus* and 7 spp. of *Bombus* were recorded. 9 of which were new to Shansi.

1951. YASUMATSU (K.), MORIMOTO (R.), IWATA (K.). — See MORIMOTO.

1951. YASUMATSU (K.), BROWN (W. L. Jr.). — *On the publication date of Polyhomoa itoi Azuma* (*Mushi*, 22, 93).

Kydris mutica Brown, *P. itoi* Azuma syn. nov.

1951. YASUMATSU (K.), BROWN (W. L. Jr.). — *Revisional notes on Camponotus herculeanus Linné and close relatives in Palaearctic region (Hym., Formicidae)* (*J. Fac. Agr., Kyushu Univ.*, 10, 29).

Eurasian spp. were revised as follows: *C. h. herculeanus*, *C. h. japonicus*, *C. igniperda*, *C. o. obscuripes*, *C. o. hemichlana* spp. nov., *C. yessensis*, *C. formosensis*, *C. vagus* with spp. inquirendæ: *C. punctatissimus*, *C. cilicicus*, *C. vagus* var. *kodorica*, *C. herc. eudokiae*.

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~~12 Nov 1954~~

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